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MARSUPIALIA, INSECTIVORA, PRIMATES, CREODONTA AND CARNIVORA FROM THE HEADON BEDS (UPPER EOCENE) OF SOUTHERN ENGLAND

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SYNOPSIS

The present work incorporates a revision of part of the mammalian fauna of the Headon Beds (Upper Eocene) of Hampshire and the Isle of Wight.

Stratigraphical and historical aspects of the main mammal-yielding horizons in the Headon Beds are presented, together with provisional lists of the complete mammalian fauna.

Marsupialia, Insectivora, Primates, Creodonta and Carnivora are considered in the systematic descriptions. Fourteen species of mammals are described, of which four are new. Two new insectivore genera, *Scraeva* and *Arvaldus* are referred to the Nyctitheriidae. *Arvaldus* is known from a single species, *A. stintoni;* two species of *Scraeva* are recognised, *S. hatherwoodensis* and *S. woodi.* A partial upper dentition has been referred to the pantolestid insectivore *Opsiclaenodon major*, previously known only from the lower dentition. Well preserved material of a new species of *Dyspterna*, *D. hopwoodi*, supports reference of the genus, formerly almost a *nomen dubium*, to the Pantolestidae, and confirms the close relationship of *Dyspterna* and *Opsiclaenodon*. *Heterohyus* sp., *Adapis parisiensis* and *Pseudoloris parvulus* all constitute new records from the Headon Beds.

The evidence from those mammals given detailed study, indicates that at present the Upper Headon Beds are best grouped provisionally with the Lower Headon Beds in the Upper Eocene (Lower Ludian). The Eocene/Oligocene boundary should be sited at some position above the Upper Headon Beds.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

The first mammals recorded from the Headon Beds were listed by Wood (1844); these specimens, listed again by Charlesworth (1845), came from the Lower Headon Beds of Hordle Cliff. In a further paper, Wood (1846–47) listed and excellently illustrated this and further material from Hordle Cliff. The first record of mammals from the Upper Headon Beds of Headon Hill was in a stratigraphical account by Prestwich (1846). The earliest detailed description of mammals from the Headon Beds was by Owen (1848).

In a preliminary paper in 1848, Barbara, Marchioness of Hastings recorded mammals from Hordle Cliff. She published, in 1852 and 1853, the results of six years' collecting from this section. In addition to mammals, the Marchioness recorded fish, reptile and bird material, together with valuable information about occurrence and preservation. Also in 1852, Wright recorded an isolated mandible from the Lower Headon Beds of Headon Hill; this was described by Owen (1857a). Some of the Marchioness of Hastings' specimens were described by Owen (1857b) and Davies (1884).

The only detailed systematic work was by Lydekker in his 'Catalogue of the Fossil Mammalia in the British Museum', published in five parts between 1885–87. The Headon Beds material was incompletely and sometimes inaccurately listed, but Lydekker made a valuable contribution, consolidating Owen's work and describing more of the Marchioness of Hastings' collection. Some of Lydekker's results were published as a few short papers (1884, 1885b, 1885d).

Stehlin's monograph 'Die Säugetiere des schweizerischen Eocaens' (1903–16) contained critical discussions of some of the Headon Beds material. In a faunal paper, Stehlin (1910) listed sixteen species from Hordle Cliff. Depéret (1917), in a revision of the mammalian fauna of Euzet-les-Bains, listed four species from Headon Hill and sixteen from Hordle Cliff. Contributions on aspects of the fauna were made by Cooper (1910, 1925, 1926, 1928). The most recent work, on isolated genera, has been by Butler (1946), Simons (1961) and Franzen (1968).

The present work comprises a revision of part of the mammalian fauna of the Headon Beds. In the faunal lists, identification of Rodentia, Perissodactyla and Artiodactyla is tentative; these elements of the Headon fauna have not yet been studied in detail.

Throughout the systematics, the age of the Headon Beds is considered provisionally as Upper Eocene (Lower Ludian). This problem is discussed later in the light of the evidence afforded by study of the mammals.

Traditional stratigraphical nomenclature has been retained for the subdivision of the succession; as the purpose of the present work is primarily palaeontological, no attempt has been made to bring this nomenclature into concordance with modern international stratigraphical practice.

The registration numbers of museum specimens are prefixed as follows:

B.M.	British Museum (Natural History)
S.M.	Sedgwick Museum, Cambridge
G.S.M.	Geological Survey Museum

D.M.S.W.	D.M.S. Watson collection; now in University Museum of Zoology, Cambridge

In addition, some specimens are from the private collection of Mr F. C. Stinton; these are prefixed F.C.S. Where differentiation of several specimens grouped under a single museum registration number has been necessary, numbers in parentheses have been added after the museum registration number.

In the tables of measurements, all dimensions are in millimetres. Antero-posterior length (a-p) and transverse width (trs) are maximum values. Measurements in parentheses represent approximations, based on damaged teeth or taken from roots.

I am very grateful to Dr R. J. G. Savage, not only for supervision of the initial research, but also for his continued encouragement, advice and stimulating discussion since that time. I also wish to thank him for so readily making available his personal library and for critically reading the draft manuscript. I am indebted also to Dr D. E. Russell for much encouragement and advice, for his generosity in permitting examination of type specimens and manuscript from unpublished work and for critically reading the draft manuscript.

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The initial research, of which this paper forms part, was carried out during the tenure of a studentship from the (then) Department of Scientific and Industrial Research. This grant and the facilities offered by the late Professor W. F. Whittard in the Geology Department of the University of Bristol are gratefully acknowledged.

II. FOSSIL HORIZONS AND FAUNAL LISTS

(a) Introduction

A general account of the geological structure and Tertiary stratigraphy of the Hampshire Basin can be found in Chatwin (1960). A brief summary of the stratigraphical subdivisions and geographical distribution of the Headon Beds is given by

Curry (1958a). Useful introductory summaries of the stratigraphy of classic Tertiary coastal sections in the area are presented by Curry (1958b and 1958c).

Mammalian material has been obtained from the brackish and freshwater Lower and Upper Headon Beds at two main localities (Fig. 1): on the mainland at Hordle Cliff (Lower Headon Beds) and on the Isle of Wight at Headon Hill (Lower and Upper Headon Beds).

The only record of a fossil mammal from the predominantly marine and estuarine Middle Headon Beds is ?*Zygorhiza juddi* (Seeley), a cetacean (Kellogg, 1936 : 176). The specimen, a caudal vertebra, was obtained from the purely marine basal Brockenhurst Bed, at Royden near Brockenhurst (Judd, 1881).

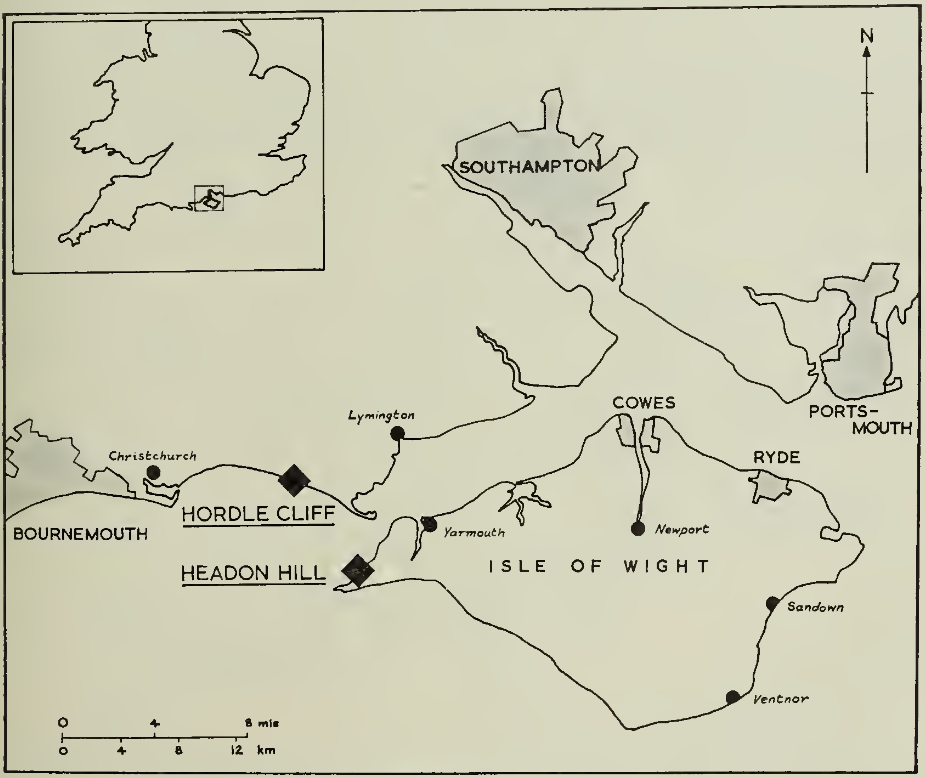

FIG. 1. Map showing the two main mammal-yielding localities of Hordle Cliff and Headon Hill.

(b) Horizons at Hordle Cliff, Hampshire

(i) Introduction

In Christchurch Bay, continuous cliffs from Mudeford eastwards to Milford-on-Sea expose excellent sections of the Barton and Lower Headon Beds, with representatives of the Bracklesham and Middle Headon Beds. The succession dips gently eastwards. The cliffs, capped by Pleistocene Plateau Gravel, range in height from 10–30 m, and are interrupted in places by small ravines or 'bunnies' as they are known locally.

The Headon Beds outcrop at Hordle Cliff (= Hordwell Cliff, the old spelling, still used occasionally) from east of Barton-on-Sea (just west of Beckton Bunny) to Milford-on-Sea (figs 2–4). In some early accounts, the section from Beckton Bunny to Long Mead End was known as Beacon Cliff, and 'Hordle Cliff' was restricted to the section from Long Mead End to Milford-on-Sea. However, for many years, all the section containing the outcrop of the Headon Beds (including Beacon Cliff) has been described as Hordle Cliff; this latter established usage is followed here.

The lowest part of the Headon Beds, the Mammal Bed, occurs beneath the Plateau Gravel west of Beckton Bunny, running obliquely down the cliffs as a vertical scar-like face, to reach sea level just east of Long Mead End. The Crocodile Bed forms a similar, higher scar. The highest beds, the *Limnaea* Marl and associated beds, outcrop as a lens below the Plateau Gravel, just east of Hordle House. At Paddy's Gap, the Milford Marine Bed represents the basal Middle Headon Beds. Over most

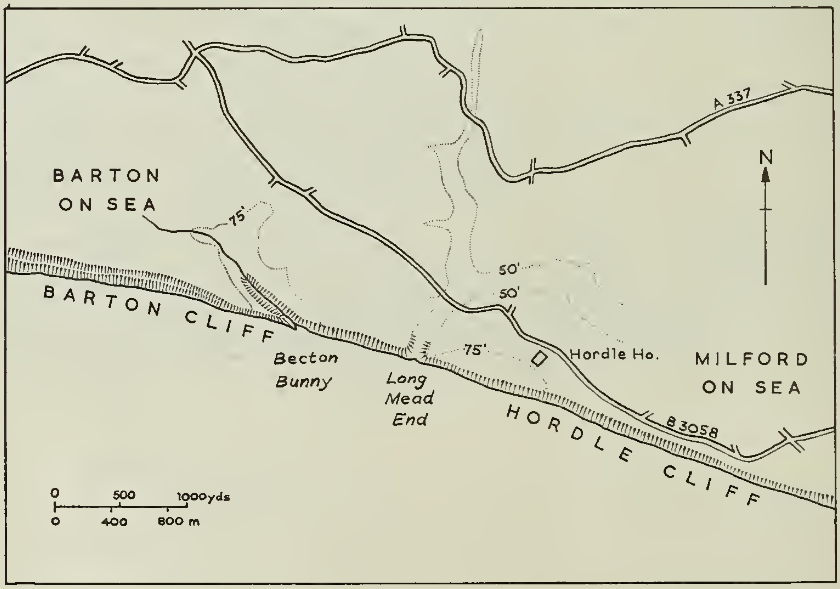

FIG. 2. Locality map of Hordle Cliff, Hampshire.

of the section, there is usually a veneer of talus and at several localities, notably at Long Mead End, there is extensive slipping; thus individual beds can be traced laterally only with difficulty.

The bulk of the museum material was obtained from the Lower Headon Beds of this area, mainly in the middle of the 19th century. The first recorded specimens, apparently derived from the Crocodile Bed, were listed by Searles Wood in 1844. The most significant contributions were made by Barbara, Marchioness of Hastings who described in 1852 and 1853 the results of six years' collecting from these beds. She made extensive collections of vertebrate remains from two main horizons, the Mammal Bed and the Crocodile Bed. Unfortunately, her material was not accurately labelled and the specimens, purchased by the British Museum (N.H.) in 1855, usually only bear the information 'Upper Eocene, Hordwell', or are listed in Lydekker's Catalogue as 'from the Headon Beds of Hordwell'. However, from the Marchioness's accounts (1848; 1852; 1853), it appears that the major mammal-yielding horizons were highly fossiliferous pockets within the Crocodile Bed. Regardless of the name given to it by later collectors, the Mammal Bed seems to have been much less important quantitively.

Many museum specimens still bear adhering matrix; this is very variable, comprising white and grey sands both coarse and fine, fine greenish-blue sandy clays, sometimes shelly, and coarse brown clayey sands. It is probable that most of the specimens with adhering greenish-blue sandy clay were obtained from the Mammal Bed, but the other lithologies are much less diagnostic. Also, matrix is no longer preserved on a considerable number of specimens. Consequently, material from these two main horizons cannot be reliably distinguished and is here considered collectively.

The Marchioness of Hastings also listed (1852; 1853) several apparently minor mammal-yielding horizons. Material from these levels was referred to only as 'bones and teeth of mammals' and 'rodent jaws'. None of the Marchioness's collection indicates derivation from any of these horizons, and the specimens, if still preserved, are presumably incorporated in the Mammal/Crocodile Bed sample. These well-defined horizons are listed below for completeness.

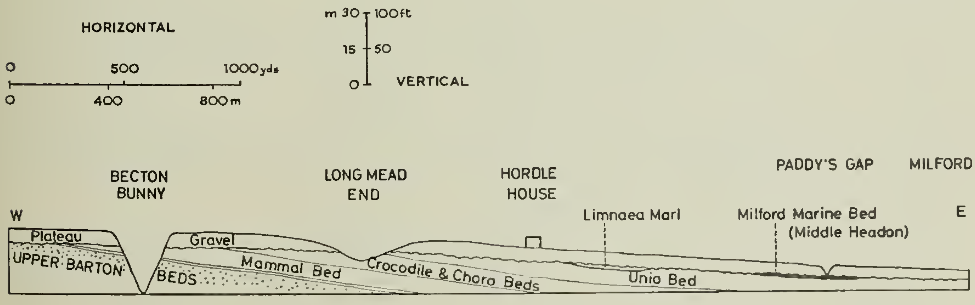

FIG. 3. Cliff section of the Lower Headon Beds at Hordle Cliff, Hampshire. Based on Curry, 1958b, fig. 1.

Little mammalian material has been found for many years from Hordle Cliff; one specimen, a mandible, was found in 1926. All these sites were examined during 1961–62, but little material was found.

All mammal-bearing horizons from the Lower Headon Beds of Hordle Cliff are listed below, together with the mammalian material derived from them. Relevant parts of the Marchioness of Hastings' descriptions are given; these quotations are taken mainly from the Marchioness's earlier detailed account (1852) in French, and not from her later, slightly modified English transcript (1853) of this paper.

(ii) Lower Headon Beds

Rodent Bed

Stratigraphy

At Hordle Cliff, a thin layer of dark clayey sand occurs almost at the top of the Lower Headon Beds, resting on a comminuted shell bed, the latter usually being known as a *Limnaea* Marl. The clayey sand is overlain by about 1 m of marl—the highest horizon referred to the Lower Headon Beds—which is stained and altered by the overlying Plateau Gravel. This *Limnaea* Marl and the overlying beds are of restricted lateral extent and outcrop immediately beneath the subhorizontal capping of Plateau Gravel just east of Hordle House, continuing eastwards for some 275 metres. Further westwards, these beds, if originally present, have been removed by erosion, although eastwards they wedge out, since at Paddy's Gap, basal Middle Headon sands rest directly on the Lower Headon *Unio* Beds.

These beds—the uppermost marl, the thin dark clayey sand and the underlying *Limnaea* Marl—were first described by the Marchioness of Hastings. Referring to her bed 1 (1852 : 194), she stated, 'La partie supérieure et principale de cet lit est entièrement dépourvue de fossiles; mais à environ un demi-mille de l'endroit où ces couches surgissent, une petite bande d'argile d'une couleur foncée, d'environ 4 pouces, se montre à la base du lit; . . .' The Marchioness listed extensive vertebrate remains, including rodent material, from this bed: '. . .; cette bande contient beaucoup de débris, mais généralement très comprimés et très fragiles. On y trouve de petites mâchoires de rongeurs, des portions de carapace et de plastron d'*Emys*, des dents et parfois beaucoup de fragments d'os de Crocodile, des vertèbres de serpents, et rarement des dents et des os de *Mammifères*.' The exact position of this small band of dark coloured clayey sand was left in no doubt by the Marchioness by her reference to the underlying *Limnaea* Marl.

Tawney & Keeping, in their detailed stratigraphical account of Hordle Cliff (1883 : 567), gave a similar description of the beds but listed only 'serpents' vertebrae' from the *Limnaea* Marl. The Marchioness's extensive list of vertebrate material from the dark clayey sand was omitted.

However, information given by Gardner, Keeping & Monckton (1888 : 596) is largely in agreement with the observations of the Marchioness; these authors recorded '. . . serpents' vertebrae, rodents' teeth, etc.' from the dark clayey sand.

The term 'Rodent Bed' was first used by Reid, (*in* Reid & Groves, 1921). This account, as Curry has observed (1958a : 69), was very confused, but Chandler who worked with Reid stated (1925 : 4) that the term was applied by him to the *Limnaea* Marl. Chandler, three years earlier (1922 : 224), recorded a section just to the east of Hordle House, in which she listed the '*Limnaea* Marl or Rodent Bed'; no vertebrate remains were noted by her from this horizon. Immediately above the *Limnaea* Marl she recorded 'a dark streak 2 in., with teeth, bones.' This latter account by Chandler was thus essentially the same as the original description by the Marchioness of Hastings. Recently, Curry (1958a and 1958b) adhered to the terminology of Reid and Chandler, referring to the *Limnaea* Marl as the 'Rodent Bed'.

Recently obtained specimens, part of an unreturned Sedgwick Museum loan, are labelled, 'Rodent Bed, Hordle Cliff, Hampshire'. This material may have been derived from the *Limnaea* Marl (Rodent Bed, *sensu stricto*) by Reid in the early years of the present century. Part of this material belonged to C. F. Cooper and may have been collected by him between the years 1910–30. However, the Marchioness's original description and some later accounts point to a possible derivation, at some time, from the overlying dark clayey sand; recent fieldwork has tended to confirm this latter view. Owing to the uncertainty of the precise horizon from which the

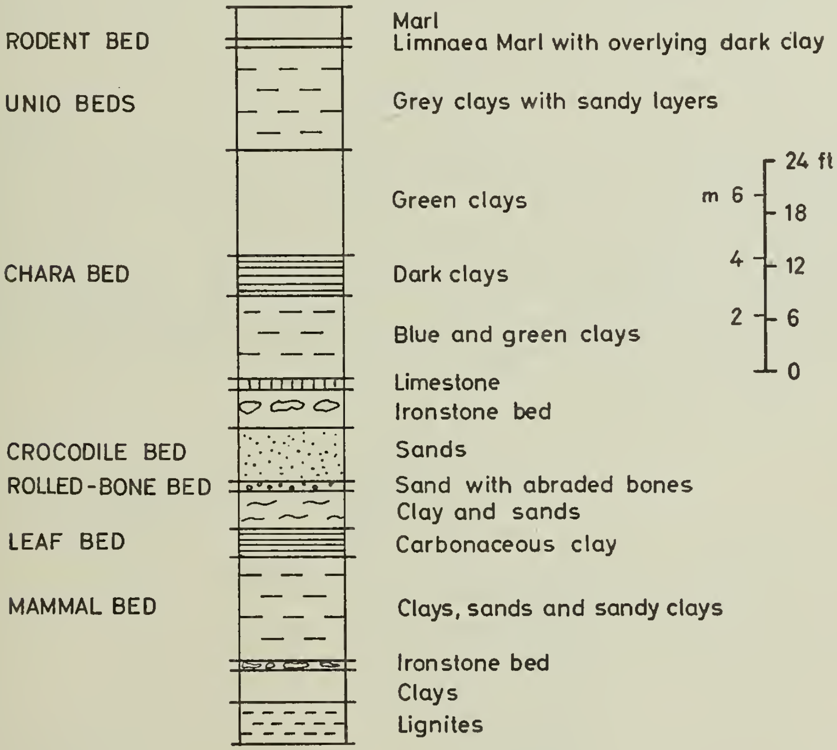

FIG. 4. Generalised succession of the Lower Headon Beds at Hordle Cliff, Hampshire. Modified from Gardner, Keeping & Monckton, 1888, fig. 4.

material was obtained, the term 'Rodent Bed' (*sensu lato*) is applied collectively here to the *Limnaea* Marl and the overlying thin dark clayey sand.

Mammalian fauna

Almost all the mammals collected from the Rodent Bed found their way to Cambridge. In 1932, C. F. Cooper, then Superintendent of the University Museum of Zoology, arranged for the material to be borrowed by M. A. C. Hinton who intended to describe them, presumably in one of his publications on rodents. Following Hinton's death in 1961, Dr R. J. G. Savage, his scientific executor, found the specimens but none of Hinton's relevant notes or manuscript. This material comprised several boxes of small isolated teeth, some of which were roughly sorted, and a few other boxes filled with unsorted bone fragments and teeth of small mammals, reptiles and fish. Most of these bones were unregistered but labelled 'Rodent Bed, Hordle Cliff, Hampshire'. The mammalian teeth (mainly rodent) have been separated from the rest of the debris, classified, and returned to the Sedgwick Museum. A few other boxes, only labelled 'Hordwell' contained fairly complete rodent maxillae and mandibles. The preservation, and adhering white sand matrix suggest derivation from the Mammal/Crocodile Bed; this material is not considered further in the present section. In a letter to Hinton, dated 22nd March 1932, Cooper remarked of the specimens he arranged to be borrowed by Hinton, '. . . some belong to the Sedgwick, some to me and one box to Watson'. This latter box, clearly marked 'property of D.M.S. Watson' has been returned to the University Museum of Zoology which now houses the Watson collection, but the specimens belonging to Cooper were not differentiated and have been returned to the Sedgwick Museum.

Screening of material at intervals along the outcrop has been carried out during recent fieldwork. Occasional rodent teeth and turtle fragments were recovered from the upper levels of the *Limnaea* Marl, and the overlying dark sandy clay has yielded a moderate quantity of small-sized vertebrate debris, including a few mammal teeth. The present rather unproductive nature of this horizon suggests that the

TABLE 1

Fauna of the Rodent Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	2
Insectivora:	*Scraeva woodi* gen. et sp. nov.	1
	Heterohyus sp.	1
	Opsiclaenodon major	1
Primates:	*Microchoerus erinaceus*	4
Rodentia:	*Adelomys ?siderolithicus*	6
	Adelomys ?depereti	1
	Adelomys sp.	3
	Theridomyid spp.	519
Artiodactyla:	*Cebochoerus* sp.	1
	Dichodon cervinum	1

'Hinton loan collection', if indubitably from this level, was collected from a fossiliferous pocket which has been since exhausted.

A complete list of the known material from this horizon is given in table 1. This material is all of very small size and evidently represents a current-sorted accumulation; all the large Headon Beds species are absent. All the specimens are fragmentary and teeth are known only in the isolated state. Some of the material is water-worn. The sample is dominated by over 500 theridomyid teeth which may be referable to more than one species.

Depositional environment

In general aspect, the association of a dark coloured clayey sand with a comminuted shell bed is remarkably similar to associated dark clayey sands and comminuted shell beds which make up the Upper Headon *Microchoerus* Bed, discussed in detail in a later section. The depositional environment is probably closely similar, both associations representing shoreline deposits of muds, sands and shell banks. Evidently, mammalian material was carried onto this shore by a river or streams. The material was then broken up and size-sorted by strong current and wave activity, the small-sized fraction being eventually incorporated in the shoreline deposits.

Crocodile Bed

Stratigraphy

This horizon, about 2·1 metres of whitish sands, lies above the Leaf Bed and almost immediately below the upper ironstone band. It was first named as such in print by Wright in 1851. The upper part is made up of fine soft white sands but the lower layers are harder and brownish in colour. West of Hordle House, the bed outcrops at the base of the cliffs, rising westwards until west of Long Mead End, it is truncated by Plateau Gravels capping the cliffs.

Mammalian material apparently from this horizon was first described in 1844 and 1846 by Searles Wood, who recorded *Palaeotherium, Dichobune, Spalacodon* and *Microchoerus*. No precise level was given in this paper, but his son, Searles V. Wood, many years later verified that this material was obtained from the Crocodile Bed (Judd, 1882 : 475, footnote). The earliest reference to mammals being collected from the Crocodile Bed was by the Marchioness of Hastings (1848).

It appears that this horizon was first worked extensively by the Marchioness of Hastings, who recorded (1852 : 198) *Paloplotherium, Dichobune* and *Hyaenodon:* 'Parmi les mammifères nous avons: le *Paloplotherium;* une belle série de mâchoires et d'os est dans une collection . . . On y rencontre également le *Dichobune,* l'*Hyaenodon.* (J'ai dans ma collection une seule mâchoire inférieure parfaitement conservée . . .)'. She also listed crocodile material, several species of *Trionyx, Emys, Lepidosteus* and bird bones.

The Marchioness observed (1852 : 197) that abundant shells invariably accompanied the vertebrate remains and that the sand surrounding the bones ' . . . devient verdâtre, d'une nature boueuse ou argileuse, . . . '. She recorded that the most richly fossiliferous level was about three feet from the top of the bed and that the middle of the outcrop, a little to the west of Hordle House, was the most productive locality. It is evident from the Marchioness's account (1852 : 198) that most of the vertebrate remains were found closely packed together, in pockets which were widely separated and of infrequent occurrence: 'Les débris de *Lepidosteus* abondent dans cette couche, et se trouvent partout, mais en très grande quantité avec les os. Généralement la où se montrent les débris d'un animal, ou en trouve d'autres qui les accompagnent, et dans un espace de 6 verges on peut trouver des débris de toutes les espèces ci-dessus mentionées. . . . Après avoir trouvé un endroit fécond, il se peut qu'on explore des certaines de verges sans rien rencontrer que quelques coquilles, quelques écailles de poissons, des graines et des plaques osseuses de peau de crocodile, débris qui sont très abondants.'

The Marchioness described one such pocket in her earliest account of the Hordle cliffs (1848 : 63): ' . . . the vertebrae and other bones of the Crocodile and Paloplotherium were found at intervals of from four inches to three feet apart to the westward of the heads . . . I must not omit likewise to state, that close to this crocodile's head (the whole group comprising a space of about six feet long by ten inches only in thickness, and following each other nearly in a straight line) were found the nearly entire shell of a fossil Trionyx . . . and the jaw, vertebrae, and scales of a fish of the order *Lepidosteus*.'

It is likely that a large part of the early museum collections came from these richly fossiliferous pockets in the Crocodile Bed which were largely worked out by the Marchioness of Hastings. As far as is known, no important mammalian material has been recorded subsequently from this horizon. Recent examination has produced only scales of *Lepisosteus* and occasional crocodile and turtle bones.

Depositional environment

No detailed examination of this horizon has been undertaken. Dr N. Edwards who has been working on the sedimentation of the Headon Beds considers (personal communication) that the Crocodile Bed was deposited near the mouth of a river. This river, inhabited by turtles, crocodiles and fish, brought in mammalian material and large quantities of detrital sediments. Estuarine elements in the molluscan fauna indicate a slight saline influence. The rich pockets of vertebrate remains worked by the Marchioness of Hastings, may have accumulated in scour channels between sand bars.

Mammal Bed

Stratigraphy

This horizon, bed No. 9 of Tawney & Keeping, comprises about 3·7 metres of bluish-green clays, white-brown sands and blue sandy clays, occurring between the Leaf Bed and the lower ironstone band. It outcrops at the base of the cliffs just west of Hordle House, running westwards to Becton Bunny, where at the top of the cliffs it is overlain by Plateau Gravel.

The first reference to mammalian material from this horizon may have been by Owen (1846 : 323) who recorded a fragmentary humerus and a lower molar of *Palaeotherium* 'from the Eocene clay at Hordwell'. Two years later, Owen (1848) described *Palaeotherium medium*, *Paloplotherium annectens* and *Dichodon cuspidatus* obtained by Falconer 'from the Eocene Sand at Hordle, Hampshire'. Although Wright (1851) stated (without giving reasons) that these specimens came from the Mammal Bed, it appears, from the accounts of the Marchioness of Hastings (1848; 1852) and Owen (1848), that some of the material was derived from the Crocodile Bed.

The Marchioness of Hastings (1852) described the Mammal Bed in detail, listing vertebrate material from the various subdivisions, although no precise localities were given. At the top, just below the Leaf Bed, the Marchioness recorded a green clay containing mammalian material. She stated (1852 : 200), 'J'ai une mâchoire inférieure très écrasée (comme tous les débris qu'on trouve dans cette partie) d'*Anthracotherium*, et probablement des portions de mâchoire inférieure de *Paloplotherium*.'

Below this clay, the Marchioness mentioned white sands containing several thin ironstone bands; the sands contained, associated with layers of shells, well preserved vertebrate remains which were not common, and were difficult to extract. She recorded, ' . . . on trouve des *Trionyx*, des *Emys*, des fragments de mâchoires des mammifères, avec des dents, des vertèbres de poissons, parfois des os, des ossements d'oiseaux, et de très petites mâchoires, mais pas de crocodiles'.

The next well-defined horizon recorded by the Marchioness was a bed of whitish-brown sand with bands of green clay in places. The upper half of this bed contained the same vertebrate material as that from the overlying bed.

The best specimens were obtained from the lowest part of the Mammal Bed—bluish-green sandy clays. The Marchioness stated (1852 : 201), 'J'ai tiré de là une dent d'*Anoplotherium* commun et une *scapula*, 2 *tibias*, 2 *Humérus*, *Métacarpes*, etc, qui sont indéterminés, mais que je crois d'*Anoplotherium*, des *Paloplotherium*, des débris de *Crocodile*, des Trionyx, des oiseaux, un très grand poisson inconnu, des Emys.'

Subsequently, the Mammal Bed has apparently yielded little material. Tawney & Keeping (1883) observed of this horizon, 'We had the good fortune to find the mandible of a *Dichodon* here on our last visit. Mammals, however, have been seldom found of late years'. A fragmentary mandible, the type of '*Hyaenodon aimi*', was discovered in 1926. No precise locality was recorded, but the specimen, according to Mr F. C. Stinton (personal communication), came from the Mammal Bed at Long Mead End. Examination of this horizon in 1961 and 1962, yielded only a single ungulate calcaneum; this came from slumped debris at Long Mead End.

Depositional environment

Dr N. Edwards has suggested (personal communication) that the Mammal Bed generally, was laid down in 'coastal fen-land waters' and probably represents various stages in a silting-up cycle from shore conditions (Long Mead End sands at the top of the Barton Beds) to swamp (Leaf Bed).

Mammalian fauna of the Mammal/Crocodile Bed

A combined list of all the mammalian material which has probably been derived from the Mammal Bed and Crocodile Bed is given in Table 2.

TABLE 2

Fauna of the Mammal/Crocodile Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	6
	'*Peratherium* species B'	4
Insectivora:	*Scraeva woodi* gen. et sp. nov.	4
	Opsiclaenodon major	21
Primates:	*Adapis magnus*	51
	Microchoerus erinaceus	45
	Pseudoloris parvulus	1
Rodentia:	*Adelomys ?depereti*	1
	Adelomys sp.	1
	Theridomyid spp.	176
Creodonta:	*Hyaenodon* c.f. *minor*	10
Carnivora:	*Quercygale hastingsiae*	1
Perissodactyla:	?*Anchilophus* sp.	2
	Plagiolophus annectens	33
	Plagiolophus minor	11
	Palaeotherium muehlbergi praecursum	6
	Palaeotherium sp.	7
Artiodactyla:	*Cebochoerus* sp.	1
	Choeropotamus depereti	1
	Dacrytherium ovinum	1
	Catodontherium sp.	2
	Haplobunodon lydekkeri	3
	Haplobunodon sp.	1
	Anthracotheroid *incertae sedis*	1
	Dichodon cuspidatus	30
	Dichodon cervinum	3
	Pseudamphimeryx hantonensis	2

Some of the material was apparently associated. Representatives of all orders, a total of 28 species, are present, of which one third are known only by single specimens; this is the most complete sample known from the Headon Beds, but as noted earlier, the material was probably collected from several distinct lithologies within a vertical interval of about 9 metres.

As with the Rodent Bed, the sample is dominated by rodents, mainly theridomyids, which make up a little under half of the sample. Primates are next in abundance, representing just under one quarter of the sample. Perissodactyls are slightly more abundant than artiodactyls, the specimens of the two orders combining to form about one quarter of the sample. The Artiodactyla show the most diversity: 10 species are present of which 5 are represented by single specimens. Insectivores, marsupials, creodonts and carnivores, in order of decreasing abundance, make up only a small fraction of the sample.

Minor horizons

Green clay (2·7 metres) below the Unio Bed

This horizon, numbered 30 by Tawney & Keeping (1883) corresponds in part, according to these authors, to bed 4 of the Marchioness of Hastings. The Marchioness mentioned small undescribed teeth and jaws of mammals obtained from sandy partings in these green clays. She stated (1852 : 195), 'Les lignes sablonneuses contiennent des *Paludina lenta*, des *Potamomya plana*, très pressées, des débris de poissons, des vertèbres et des écailles, de petites dents de *mammifères* non décrits, avec de très petites mâchoires. J'ai un grand *calcaneum* trouvé dans cette couche: c'est le seul grand os qu'on y ait jamais rencontré.'

An isolated theridomyid upper incisor, part of the Hinton loan of Hordle rodent material, is labelled '6 feet below *Limnocarpus* Bed'. The term '*Limnocarpus* Band' was first applied by Chandler (1922 : 224) to a thin bed rich in seeds of *Limnocarpus*, situated near the base of the *Unio* Bed. As the *Unio* Bed (Bed 31 of Tawney & Keeping, 1883) is about 2·4 metres thick, this tooth probably came from the green clays below, close to the Marchioness's original horizon.

Rolled-bone Bed

This horizon, so named by Tawney & Keeping (1883) because of the worn appearance of its vertebrate content, was listed by them as bed No. 13. This apparently corresponds to part of the Marchioness's bed No. 11. It is composed of 0·15–0·23 metres of greyish-white sands, occurring just below the base of the Crocodile Bed.

The Marchioness of Hastings recorded worn bones of rodents and other mammals from this horizon. In 1852 (p. 199) she wrote, ' . . . ; on y trouve aussi en assez grande abondance des os roulés d'*Emys*, de *Trionyx*, *Crocodile*, *Rongeurs*, des vertèbres de poissons, d'oiseaux et de mammifères.' She observed that the best preserved specimens were mammalian teeth which were sometimes nearly intact; the rest of the material was rounded and hardly recognisable.

Whitish sand above the Leaf Bed

The Leaf Bed, numbered 10 by Tawney & Keeping, is a plant-bearing carbonaceous clay, 0·23–0·46 metres thick, occurring between the Crocodile Bed and the Mammal Bed. Immediately overlying this Leaf Bed, is a whitish sand (No. 11 of Tawney & Keepings' account), from the base of which, the Marchioness of Hastings recorded an associated group of palaeotheroid bones. She stated (1852 : 199), ' . . . , à la base de la couche, et près de son extrémité, on a trouvé dans l'espace de quelques verges environ 30 os, appartenant évidemment au même animal, un *Palaeotheroide*.'

Thin shell bed above the Lower Ironstone Band

This horizon occurs immediately above the ironstone band (numbered 8 in Tawney & Keepings' section), which is usually considered to mark the base of the Mammal

Bed. It is included here as a distinct horizon, because it has been so well defined by the Marchioness of Hastings and its mammalian content is very similar to that of a bed below the ironstone band (see below). Amongst the vertebrate material obtained from this horizon, the Marchioness (1852 : 201) listed mammalian teeth and rodent jaws: 'On y trouve également des vertèbres de serpents et de lézards, des dents de mammifères, des mâchoires de rongeurs, des écailles et des vertèbres de poissons, des débris de crocodiles, de *Trionyx* et d'*Emys*, et parfois des os plus gros et même conservés, comme des astragales et des os du carpe.'

Thin white sandy marl below the Lower Ironstone Band

This was listed by Tawney & Keeping as bed No. 7 and was stated by them to be 1 inch thick. The Marchioness mentioned that this bed contained about the same vertebrate material as that recorded from the horizon immediately above the ironstone.

(c) Horizons at Headon Hill, Isle of Wight

(i) Introduction

The Reading Beds-Barton Clay are traditionally considered as being in Alum Bay, and the Headon Hill Sands (Barton Sands) and higher beds are referred to Headon Hill, although the section is continuous.

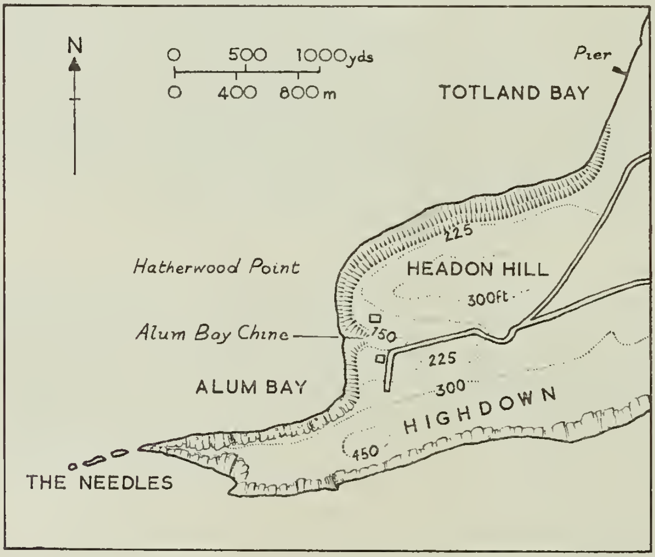

Fig. 5. Locality map of Alum Bay and Headon Hill, Isle of Wight.

Alum Bay is bounded to the south by the almost vertical Chalk ridge of High Down which terminates westwards in the Needles. The Reading Beds-Barton Clay are almost vertical, but in the upper part of the Barton Clay and in the overlying Headon Hill Sands situated immediately north of the mouth of Alum Bay Chine, the dip changes rapidly (in less than one hundred metres laterally) from vertical to horizontal (figs 5 and 6). The seaward face of Headon Hill is composed of the overlying nearly horizontal Headon and Osborne Beds, forming the lower limb of the monocline. The summit of the Hill is capped by Plateau Gravel.

The soft sands and clays of the vertical Alum Bay section form a high very steep sea cliff which is retreating rapidly due to natural erosion and the activities of coloured-sand collectors. By contrast, the seaward face of Headon Hill is relatively more gently inclined, receding inland to the summit of the hill as a series of inclined 'steps'. These 'steps', caused by the erosion of soft sands and clays occurring between bands of limestone, are usually covered by thick scree and mud-flow deposits, and often support a partial cover of vegetation. As a result, exposures here are usually discontinuous and short-lived. The relatively more resistant limestone bands stand out as scar-like cliffs in the side of the hill. The highest of these cliffs is formed by the limestone in the Osborne Beds (near the middle of the Osborne Beds); the middle cliff by the Upper Headon Limestone (at the base of the Upper Headon Beds), and the lowest and smallest cliff by the How Ledge Limestone (at the top of the Lower Headon Beds). A generalised section of the Headon Beds at the south-west corner of Headon Hill, is given in fig. 7.

By comparison with Hordle Cliff, little mammalian material has come from the Headon Hill horizons. Until recently, a jaw of *Dichodon* was the only recorded specimen (Wright, 1851a, 1852) from the Lower Headon Beds in this area. The only precise reference to mammalian material from the Upper Headon Beds of Headon Hill, was by Prestwich (1846) who listed bones and teeth of *Palaeotherium* from the Upper Headon Limestone above and below the Lignite Bed; these specimens are apparently lost.

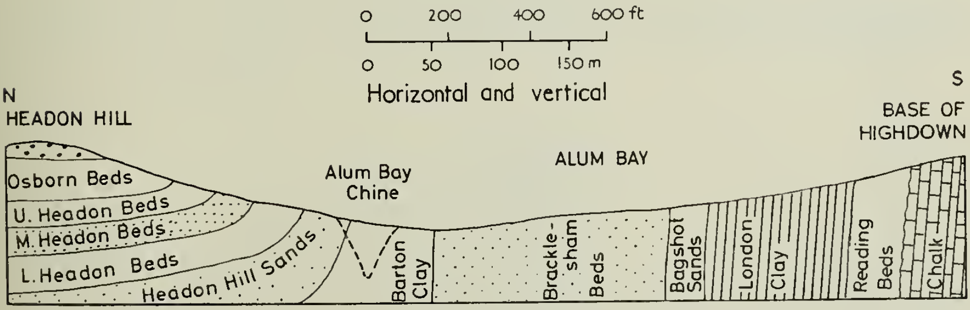

FIG. 6. Cliff section at Alum Bay and Headon Hill, Isle of Wight, showing the Reading Beds—Headon Beds. Based on Curry, 1958c, fig. 2.

Several museum specimens of *Dichodon*, *Haplobunodon* and a theridomyid are labelled 'Isle of Wight' or 'Eocene? North-west coast of the Isle of Wight', and Lydekker (1885c) listed *Dichodon* and *Dacrytherium* specimens from the 'Headon Beds, Isle of Wight'. White sand matrix adhering to some specimens, and the

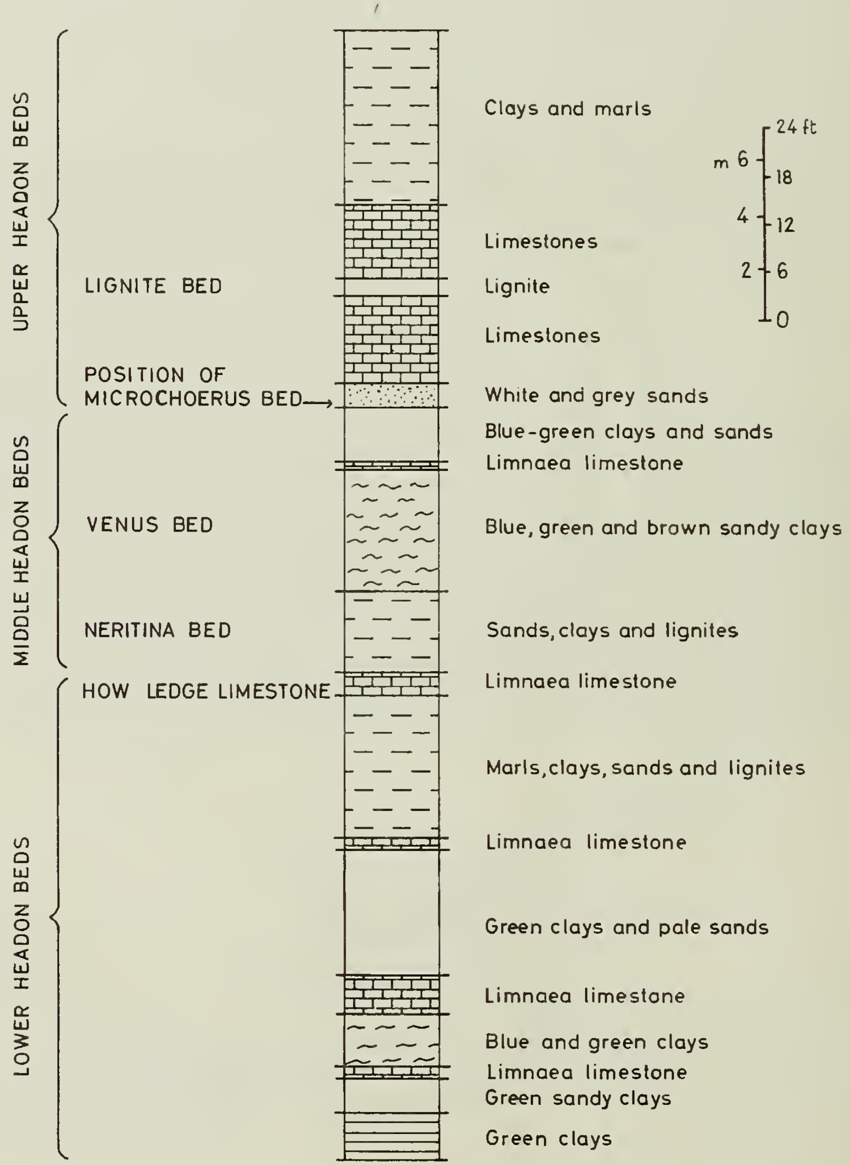

FIG. 7. Generalized succession of the Headon Beds at the south-west corner of Headon Hill, Isle of Wight.

above information from museum labels or Lydekker's Catalogue, point to derivation from the Lower Headon Beds. Two unlabelled theridomyid teeth have an adhering matrix of soft marly limestone, suggesting a probable derivation from either the Upper Headon Limestone or the Lower Headon How Ledge Limestone of Headon Hill. As the precise horizons of all this material are not known with certainty, the specimens are not included in the faunal lists.

One specimen, a palatal fragment of *Palaeotherium*, although listed by Lydekker (1886) as 'from the Isle of Wight. No history' is embedded in a shelly lignite with an associated soft shelly limestone; this matrix strongly suggests derivation from the Upper Headon Lignite Bed. Owing to the distinctive lithology of the matrix, this conclusion is considered reliable and the specimen is included in the faunal lists, constituting an isolated early record from the Lignite Bed.

In the last few years, further mammalian material has been obtained from the Lignite Bed in moderate quantity and a new mammal-yielding horizon below this, at the base of the Upper Headon Beds, has been discovered during recent fieldwork. In 1961, a mammal-bearing horizon was found near the top of the Lower Headon Beds.

Recorded below are all the definite mammal-yielding localities at Headon Hill, together with lists of mammalian material collected from them.

(ii) Lower Headon Beds

Minor horizons

Green clay, 2·1 metres above the top of the Headon Hill Sands

This horizon, recorded by Wright (1851 : 25 and 1852 : 87), yielded one specimen, a fragmentary mandibular ramus of *Dichodon cuspidatus*. Recent examination of this bed at the south-west corner of Headon Hill, has not produced further material.

Green marl immediately below the How Ledge Limestone

The post-cranial skeleton of a small mammal was obtained recently by Dr N. Edwards from this horizon at the south-west corner of Headon Hill. The specimen has not yet been described.

(iii) Upper Headon Beds

Microchoerus Bed

Stratigraphy

The *Microchoerus* Bed, named from the first mammal found, is a small lenticular horizon at the junction of the marine Middle Headon Beds and the freshwater Upper Headon Beds, at the south-west corner of Headon Hill. The lateral extent of this lens, which outcrops along the base of the Upper Headon Limestone cliff, is about 100 m (fig. 8).

A section through the thickest development (about 0·33 m) shows:

Purple and grey clay	0·10 m
Purple clayey sand	
Comminuted shell bed	0·15 m
Buff clayey sand	0·08 m

The *Microchoerus* Bed is overlain by white unfossiliferous sands, generally considered of Upper Headon age. The lowest part of the *Microchoerus* Bed, a buff clayey sand, rests abruptly on a comminuted shell bed which grades down vertically and passes laterally into a shelly blue-green clay. The shell bed and shelly clay both contain a marine fauna, including foraminiferida, and thus are best considered as Middle Headon in age. The *Microchoerus* Bed containing terrestrial detritus, forms a fairly distinct unit which is referred to the Upper Headon Beds.

The buff clayey sand, containing wood fragments and mammalian material, lies on an irregular upper surface of the lower comminuted shell bed. The upper surface of the buff clayey sand is irregular and in places, strongly fissured. The comminuted shell bed is composed mainly of fragments of lamellibranchs (?*Corbicula obovata*, *Sinodia suborbicularis*) with a few gastropod fragments (*Batillaria concava*). The bed is very lenticular, infilling hollows in the underlying sand; occasionally it is completely absent. In places, small lenses of sand are incorporated in the base. The purple sand and clay, containing mammalian material and wood fragments,

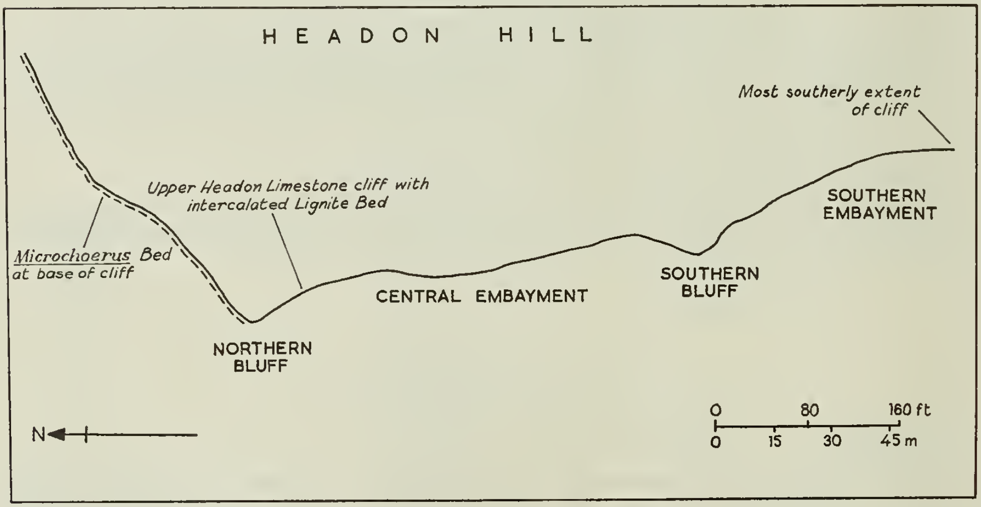
HEADON HILL
Most southerly extent of cliff
Upper Headon Limestone cliff with intercalated Lignite Bed
Microchoerus Bed at base of cliff
NORTHERN BLUFF
CENTRAL EMBAYMENT
SOUTHERN BLUFF
SOUTHERN EMBAYMENT
N
0 80 160 ft
0 15 30 45 m

Fig. 8. Map showing location of the *Microchoerus* Bed and Lignite Bed at Headon Hill, Isle of Wight. Based on a plan of the top of the Upper Headon Limestone cliff, at its most southerly outcrop on Headon Hill.

infills irregularities in the underlying shell bed. Where the latter is absent, it directly overlies the buff sand; here, shell material and lenses of buff sand are incorporated in the base of the purple sand.

Mammalian fauna

During 1962, attention was focussed on the *Microchoerus* Bed by the discovery of fragmentary mandibles of *Microchoerus* and *Scraeva* gen. nov. in the intermixed purple and buff clayey sand in the northern part of the outcrop.

The following summer, excavations were made at intervals along this part of the outcrop. About 12 m laterally was exposed and examined by handpicking and screening of the residues. Unfortunately this horizon could be followed back into the cliff for only one metre; extensive white sand overburden and overhanging limestone made further development impracticable. A badly crushed fragmentary mandible of *Catodontherium* was discovered in the iron-stained lower part of the white sand immediately overlying the *Microchoerus* Bed. A fragmentary mandibular ramus of *Peratherium* was one of several specimens obtained from a pocket of the buff clayey sand; it was badly crushed and had lost all teeth except M3, presumably during transport. The root tips of this tooth were just lodged in the alveoli, the displacement being evidently a result of final impact with the substratum before burial. The intermixed purple and buff clayey sand yield 12 isolated, randomly orientated upper teeth of a palaeothere, ?*Palaeotherium muehlbergi praecursum*. These teeth with parts of the maxillae and palate were spread over about 0·30 m. It is likely that the strong current activity during the deposition of the purple clayey sand caused fragmentation of the original palatal specimen.

TABLE 3

Fauna of the *Microchoerus* Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	1
Insectivora:	*Scraeva hatherwoodensis* gen. et sp. nov.	1
Primates:	*Microchoerus erinaceus*	1
Rodentia:	Theridomyid sp.	6
Perissodactyla:	?*Palaeotherium muehlbergi praecursum*	1
Artiodactyla:	*Catodontherium* sp.	1

A list of all material obtained from this horizon is given in Table 3. This sample is incomplete both in numbers of species and frequency of individuals. Creodonts and carnivores are absent; all other orders, except the rodents, are known only by single specimens. This is probably largely due to incomplete sampling, but as most of the specimens are of small size, is probably also affected by preferential current-sorting.

Depositional environment

The *Microchoerus* Bed evidently represents shoreline deposits left behind by the retreating Middle Headon Sea. Limited evidence from the deposition of the various individual beds in the northern part of the outcrop, suggests that the present-day cliff section represents an approximate cross section through this shoreline which trended roughly east-south-east to west-north-west. Terrestrial detritus such as wood and vertebrate remains (mainly mammalian) was carried into the brackish sea by streams to be incorporated in the shore deposits. Possibly at low water, these deposits were exposed on the foreshore as irregular spreads of mud and sand which occasionally dried out forming shrinkage cracks in the upper layers. Through strong wave activity, irregular spreads of comminuted shells accumulated in places as lenticular shell banks. General intermixing of sediments, balled-up clay pellets, scoured surfaces and broken-up mammalian remains, all testify to the erosive effect of strong current activity during the deposition of most of the *Microchoerus* Bed.

Lignite Bed

Stratigraphy

This horizon occurs within the Upper Headon Limestone, outcropping about a third of the way up the vertical cliff formed by the limestone on the south-west seaward face of Headon Hill; the lignite mainly infills an irregular erosion surface in the underlying limestone. Where the Lignite Bed is well developed, it is affected by small-scale block faulting and other post-depositional compaction phenomena.

The position of the main outcrop of the Lignite Bed is indicated on a plan showing the top of the Upper Headon Limestone cliff as it appeared in 1963 (fig. 8). At the most southerly extent of this cliff, just north of Alum Bay Chine, the beds dip northwards at about 40° as they become involved in the middle limb of the main Isle of Wight monocline; further north the beds are approximately horizontal.

The Lignite Bed and associated limestones were described by Jackson (1924). In earlier stratigraphical accounts, the bed had been largely unnoticed; it was mentioned by Judd (1880) and Lee (1881). This was accounted for by Jackson who suggested (1924 : 278) that as the deposits appear to thin towards the face of the cliff 'hence they were probably less conspicuous in times past'. This view is supported to some extent by the present distribution of the Lignite Bed: where the limestone cliff at present forms projecting bluffs, the lignite is very thin or absent, and the thickest development is in the intervening embayments.

In many places the Lignite Bed is intimately associated with the underlying limestone; this limestone is very variable lithologically and several subdivisions were recognised by Jackson (1924). The commonest type (this overlies the Lignite Bed also) is a soft impure orange marly limestone with abundant shalls of *Galba* spp. and *Planorbina* spp., fragments of turtle bones and more rarely, fragmentary mammalian remains.

A general section through the thickest development of the Lignite Bed in the southern embayment is as follows:

Lignitic shell marl	0·23 m
Hard black carbonaceous clay	0·15 m

The carbonaceous clay contains seams of shell debris and infills irregular curved fissures in the underlying marl, which often penetrate the marl to a depth of 0·61 m. The overlying lignitic shell marl is made up of comminuted shells (*Galba* spp. and *Planorbina* spp.) with thin partings of friable lignite. In the extreme south, no erosion surface is evident and the lower marly limestone passes up through a thin shell marl (representing the Lignite Bed) into the upper marly limestone.

In the central embayment, the Lignite Bed consists of the following:

Friable black lignite	0·08 m
Laminated lignitic shell marl	0·15 m
Friable black/brown lignite	0·43 m

The friable black/brown lignite in many places infills solution channels excavated usually in the soft underlying marly limestone; hard white nodular limestone bands often project into the lignite as isolated residual solutioned blocks. These solution channels are up to 0·30 m deep and appear to trend north-west to south-east. Occasional lignite-filled fissures penetrate deeply into the marl (up to 1·2 m in the northern part of the embayment). The overlying lignitic shell marl probably corresponds to the lignitic shell marl of the southern embayment; it contains several partings of friable lignite, two of which form distinct bands. This shell marl rests directly on a smooth solutioned surface of hard limestone at the southern bluff. Near the northern bluff, a shelly black lignitic clay infills smooth funnel-like sub-horizontal potholes in the underlying hard rubbly and marly limestones; these potholes trend north-south. In this area, several minor lignitic lenses occur in the limestones above and below the main Lignite Bed. At the northern bluff, the upper and lower limestones are only separated by an undulating erosion surface and the Lignite Bed has largely disappeared. Further north of this, the horizon either persists as a thin lignitic shell bed or its position is indicated by an erosion surface.

Throughout the Lignite Bed, the beds of shell marl and lenses of shell debris are made up mainly of flattened *Galba* spp. and *Planorbina* spp. Isolated crocodile teeth (*Diplocynodon* sp.) and dermal scutes and other bones of turtles (*Emys* sp.) occur sporadically throughout the horizon, both in the friable lignite and the shell marls. One small badly preserved jaw fragment, ?fish, was obtained from the top friable lignite in the southern part of the outcrop. Samples of lignite were sent to Dr J. M. Pallot for pollen analysis; pollen was identified only from a restricted range of woodland trees: *Pinus*, *Myrica* and *Engelhardtia* (personal communication).

Depositional environment

The previously described *Microchoerus* Bed apparently represents shoreline deposits left behind by a receding Middle Headon sea. After this regression, freshwater lagoonal conditions prevailed in the area, with extensive terrestrial detritus, including mammalian remains, being supplied by some fluviatile agency. Initially, sand was carried into these lagoons and spread over the abandoned muds, sands and shell banks of the retreating sea. This was soon followed by extensive carbonate deposition. The waters of the lagoons were colonised by molluscs, crocodiles and turtles;

at times growth of algae took place. Breccias, conglomerates, nodular and rubbly limestones indicate extensive penecontemporaneous erosion during the carbonate deposition. With shifting of these waters, parts of the lagoonal floor became exposed at times, drying of the sediments causing the formation of deep shrinkage fissures; elsewhere, the surface became trenched with a system of terrestrial streams which scoured out deep channels in the soft semi-consolidated marl. Hollows, potholes, and rounded surfaces were formed in the harder limestone bands by solutioning. The agency of terrestrial stream erosion was first suggested by Jackson (1924 : 278). The erosion of about 1 m of lagoonal sediments resulted in the formation of hollows, e.g. at the present-day central embayment. The southern part of the area may have been covered by shallow lagoonal waters for most of this time.

With the return of lagoonal conditions, considerable quantities of woodland vegetation were carried into these erosion hollows, to accumulate first in the fissures and scour channels. At times there were influxes of fine detrital material, resulting in the accumulation of carbonaceous muds. Periodically spreads of shells were concentrated by current activity and incorporated amongst the vegetable debris.

Mammalian fauna

With the exceptions of one specimen recorded by Lydekker (1886) and the unlocated specimens listed earlier by Prestwich (1846), all the material has been collected within the last decade. Jackson (1924) recorded the complete absence of vertebrate material.

This horizon was first examined by the author in 1961. In the following two years, a series of excavations were made at intervals along the outcrop of the Lignite Bed. About 9 m laterally was examined in this way but because of the intercalation of the lignite between relatively hard limestones, the bed could only be followed into the cliff for about 1m.

Some interesting, though not very abundant material was found: in the northern part of the main outcrop, two associated lower teeth of *Dyspterna hopwoodi* sp. nov. were obtained from a thin friable lignite overlying infilled solution hollows. The thick development of the lignite in the central part of the outcrop yielded several partially-associated long bones and a scapula, probably of a palaeothere. These bones, from the uppermost friable lignite, were fragmentary, randomly-orientated and much decomposed; they occurred within an area of about 1 m and almost certainly belonged to a single individual. At the same locality, a mandible of *Dyspterna hopwoodi* sp. nov. was found in the underlying main lignitic shell marl. Several associated upper teeth of *Palaeotherium* were discovered in the lowermost black friable lignite in the same area. Three of these teeth (P^1–P^3) were closely associated with the powdery remains of bone fragments; an isolated M^3 from about 0·15 m away, probably belonged to the same individual.

A complete list of the mammalian fauna from this horizon (and associated limestones) is presented in Table 4. The species list is more extensive than that of the *Microchoerus* Bed and all orders except the Creodonta and Marsupialia are represented by more than one species. The sample is incomplete, and the frequency of individuals is very low, most species being represented only by single specimens.

TABLE 4

Fauna of the Lignite Bed

		Numbers of specimens
Marsupialia:	'*Peratherium* species A'	1
Insectivora:	*Arvaldus stintoni* gen. et sp. nov.	1
	Dyspterna hopwoodi sp. nov.	3
Primates:	*Adapis parisiensis*	1
	Microchoerus erinaceus	1
Rodentia:	*Adelomys siderolithicus*	1
	Theridomyid sp.	7
Creodonta:	*Hyaenodon* c.f. *minor*	1
Perissodactyla:	*Plagiolophus annectens*	1
	Palaeotherium muehlbergi muehlbergi	1
	Palaeotherium muehlbergi praecursum	5
	Palaeotherium sp.	1
Artiodactyla:	*Dichodon cuspidatus*	1
	Haplobunodon lydekkeri	1

Much of the small material was collected by Mr F. C. Stinton by screening the main lignitic shell bed (personal communication); these specimens probably represent a current-sorted accumulation. With the other larger-sized material from the friable brown lignite and the black shelly lignitic clay, no current sorting is evident, and the partially-associated bones probably indicate more tranquil conditions of deposition.

Mammalian material is consistently but sparsely distributed throughout the Lignite Bed and processing of a large volume of sediment is necessary to obtain an adequate sample. As the bed outcrops in a vertical cliff, intercalated between relatively hard limestones, extensive working of this horizon is rendered difficult. In spite of these practical difficulties, the Lignite Bed remains potentially one of the most favourable sites for further development.

III. SYSTEMATIC DESCRIPTIONS

Order MARSUPIALIA

Family **DIDELPHIDAE** Gray, 1821

DIAGNOSIS. Small polyprotodont marsupials. Dental formula $\frac{5-?}{4-3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{4}{4}$. Incisors all small. Canines large. Premolars simple, trenchant or bulbous. Lower molars tuberculo-sectorial with three trigonid cusps and basined heels with hypoconulid postero-internal, near entoconid. Upper molars trigonal, with no true hypocone, external cingulum wide, with various well-defined marginal cusps (styles). Quadrupedal, plantigrade, usually with opposable hallux and pollex, often with prehensile tail (from Simpson, 1929, and 1935a : 136).

REMARKS. The generally accepted subdivision of the family is that of Simpson (1935a). Four subfamilies are recognised: Pediomyinae Simpson, 1927; Thlaeodontinae Hay, 1930; Microbiotheriinae Simpson, 1929 and Didelphinae Simpson, 1927.

Subfamily **DIDELPHINAE** Simpson, 1927

Diagnosis. Premolars trenchant. Paracone much reduced, except on M^4. Marked metastylar spur. Style B large, D smaller than C. Paraconule reduced or absent (modified from Simpson, 1935 ; 137).

Remarks. Distinguished from the other subfamilies as follows: In the Microbiotheriinae, the styles are weak and there is no distinct metastylar spur; M_4 is reduced and more simple. The Thlaeodontinae have bulbous crushing premolars; the paracone and metacone are subequal and there is no distinct metastylar spur. In the Pediomyinae, the paracone and metacone are subequal; style B is weak with D larger than C, and there is a definite paraconule.

The Didelphinae ranges from the Early Palaeocene—Early Miocene of North America; ?Palaeocene, Early Eocene—Miocene of Europe; Pliocene—Recent of South America and Pleistocene—Recent of North America. The genera currently grouped in the subfamily are as listed by Simpson (1945) with the addition of two North American forms: *Herpetotherium* Cope, 1873, from the Early/Middle Oligocene and *Didelphidectes* Hough, 1961, from the Early Oligocene.

The structure of the lower molars in didelphines is remarkably uniform and on this basis, early Tertiary forms can barely be distinguished from the living representatives of the group, the American opossums. Unfortunately, most fossil didelphines are known from fragmentary mandibles and satisfactory generic separation is difficult; the subfamily clearly needs a thorough revision.

Genus ***PERATHERIUM*** Aymard, 1850

Type species. *Peratherium crassum* (Aymard, 1846). Early Oligocene ('Sannoisian') Ronzon, France. The specimen is apparently lost.

Remarks. The genus *Peratherium* is known from the Eocene—Miocene of Europe and North America; it is the only fossil didelphine genus recorded from Europe.

Hough (1961 : 221) revived Cope's genus *Herpetotherium*, to receive certain American species, previously described as '*Peratherium*', having an uninflected angular process. The remaining American species of *Peratherium* (with inflected angulars) appear to be generically indistinguishable, on the basis of lower dentitions, from the European material and from living representatives. However, the extensive range and geographical distribution of this genus, make it likely that a better knowledge of the upper dentition of these forms will reveal several distinct genera.

About 30 species are described from Europe and about 12 from North America. Most of the European species (recently listed in Quinet & Misonne, 1967 : 5) are based on mandibular fragments, but several of the American forms are known only from upper dentitions. Of the European species, only about half of the types have been located in various museums. Many of the early types of species erected by Filhol, Blainville, Aymard and Gervais apparently are lost and the original figures and descriptions are now inadequate for detailed comparison. Examination of recent didelphid material (Hough, 1961 : 219) reveals much individual variation, together with sex and age differences within a single species. Undoubtedly, many European species distinguished mainly on size are invalid. Crochet (1969) recognised four European species of *Peratherium* of which two, *P. laurillardi* Gervais, 1848–52 and *P. cuvieri* Fischer, 1829, are known from the Ludian.

As the genus *Peratherium* is being revised by Herr W. v. Koenigswald at München[1], no diagnoses are given here; the Headon Beds material is designated merely as '*Peratherium* species A' and '*Peratherium* species B'.

'***Peratherium*** species A'

(Text-figs 9–11)

MATERIAL. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where otherwise stated.

B.M. 30350. Fragment of right mandibular ramus with M_2–M_4. The angular process and the basal part of the coronoid are preserved.

S.M. C30707. Fragment of right mandibular ramus with P_2–M_4, and alveoli of I_1–P_1. Symphysis is preserved. Associated posterior region of mandible almost complete—from same individual?

S.M. C30708. Fragment of left mandibular ramus with M_3 and parts of alveoli of M_2 and M_4.

S.M. C53476. Fragment of left mandibular ramus with M_2–M_3 and alveoli of M_4. Base of coronoid preserved.

B.M. 36812b. Isolated right M_4. Unworn.

B.M. 30348. Fragment of right mandibular ramus with M_3–M_4 and alveoli of P_2–M_2. Teeth well worn.

B.M. M26050. Fragment of right mandibular ramus with M_3. The tips of the roots just rest in the alveoli. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

F.C.S. 2. Isolated right M_3. Upper Headon Beds (Lignite Bed), Headon Hill.

S.M. C54170. Isolated left M^2. Fairly well worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

S.M. C54171. Isolated left M^3. Almost unworn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. In S.M. C30707, the jaw is long and slender. The posterior mental foramen lies below M_1 and the anterior mental foramen below P_2. The subhorizontal symphysial surface occupies only the basal half of the mandible; it has a ridged upper margin and extends posteriorly to below P_2. Two internally-situated nutrient foramina are visible: the larger foramen opens through the symphysial surface into the posterior part of the canine alveolus; slightly anterior to this, the smaller foramen lies above the symphysial surface. The recent opossum, *Didelphis*, has similar nutrient foramina. In this and other recent didelphines, the symphysis is not rigidly fused and relative movement of the two rami can take place. The foramina supply small blood vessels to connective tissue around the two symphysial surfaces. A similar condition evidently existed in these fossil forms.

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[1] Since this manuscript was submitted, the author's attention has been drawn to a paper by Von Koenigswald (1970). In this work, the cranial anatomy of *Peratherium* is compared with that of recent didelphids and the various species from the Upper Oligocene and Miocene of Europe are described.

Except for S.M. C30707, little of the posterior part of the mandible is preserved. In B.M. 30350 and S.M. C53476, the base of the masseteric fossa is preserved, bounded by strong condyloid and coronid crests. The mandibular foramen lies just below alveolar level. In B.M. 30350, the base of the angular process is inturned and shelf-like. S.M. C30707 comprises two fragments joined posterior to M_4. The fit is not good and both pieces may not belong to the same individual. The posterior region,

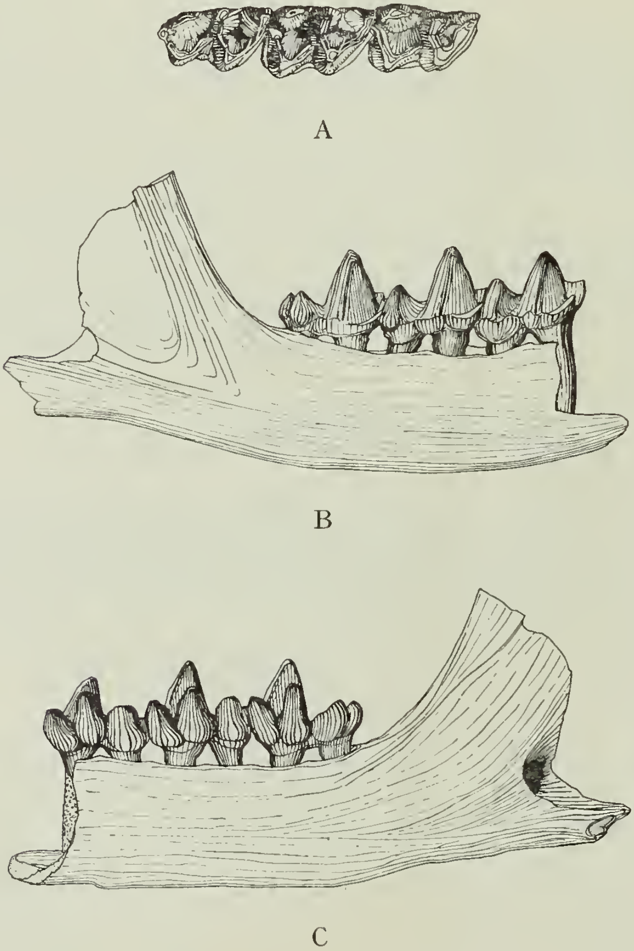

Fig. 9. '*Peratherium* species A'. Fragmentary right mandibular ramus with M_2–M_4. B.M. 30350 ×8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

however, on size can be assigned to this species although there are structural differences from B.M. 30350 which may be due to variation in individual age: the coronoid process slopes more gently; the mandibular foramen is more baso-anteriorly sited and there is a larger space between the coronoid and M_4. The convex transversely-elongated condyle lies just above alveolar level (S.M. C30707) and is separated from the coronoid by a prominent notch.

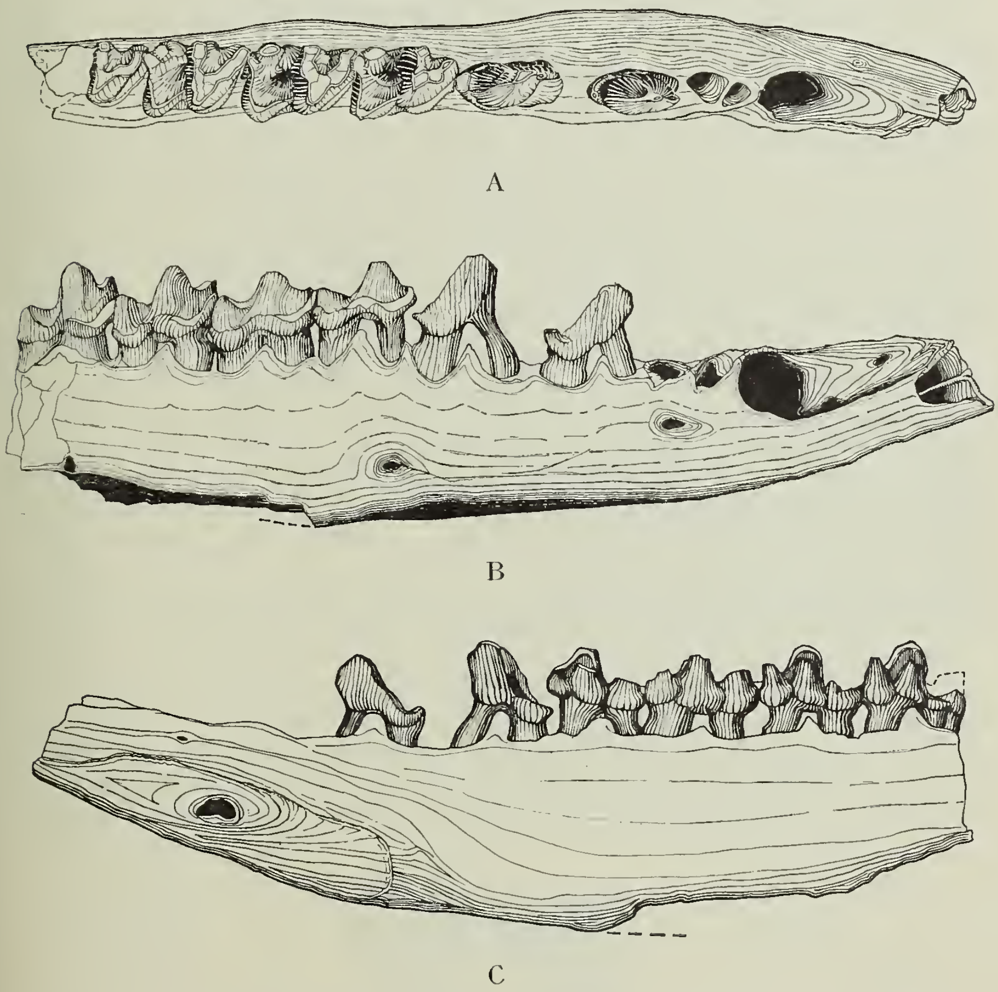

Fig. 10. '*Peratherium* species A'. Fragmentary right mandibular ramus with P_2–M_4. S.M.C30707 approx. × 8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (c) Internal view.

The four molars form a continuous series internally, the hypoconulid of one molar fitting closely against the external cingulum of the adjacent posterior tooth. M_1–M_3 are subequal in size; M_4 is of similar length but with a narrower talonid. M_4 is rectangular in outline with subequal talonid and trigonid. The trigonid is only moderately elevated, the posterior wall falling steeply to the basined talonid. The protoconid is the largest cusp, the metaconid intermediate and the paraconid smallest. There is a prominent antero-external cingulum. The paraconid, which forms the sharp antero-internal extremity of the tooth, is strongly internal, lying on an antero-posterior line with the metaconid and entoconid; it is completely separated from the metaconid. The deeply-basined talonid bears a subequal hypoconid and entoconid and a smaller hypoconulid; this hypoconulid is intermediate between the median and internal positions and posterior to the hypoconid and entoconid. A small antero-posterior crest runs from the entoconid to the posterior trigonid wall from which it is separated by a small valley. Similar crests connect the hypoconulid to the hypoconid and entoconid. There is a small crista obliqua. A strong antero-external cingulum is pressed up against and external to the projecting hypoconulid of the anterior tooth; it runs below the protoconid and hypoconid, to the base of the hypoconulid. M_3 is structurally almost identical with M_4, except that the tooth is somewhat wider transversely. M_2 is structurally nearly identical with M_3. M_1 is similar but a little smaller in size.

P_3 bears a prominent single anterior cusp which is crested anteriorly. Posteriorly two crests fall from the cusp to a small internally-shifted talonid. P_2 is smaller but structurally very similar to P_3 and separated from it by a marked diastema. P_1 is separated from P_2 by a small diastema; the tooth is represented in S.M. C30707 by two alveoli, the anterior one situated rather external to the tooth row. In S.M. C30707 the canine alveolus indicates a large semi-procumbent tooth. Anterior to this, a large alveolus subdivided into three, may indicate the positions of three closely-spaced incisors.

Two isolated upper teeth considered as M^2 and M^3 are known from the Headon Beds. M^3 is distinguished from M^2 by having a sharper internal apex and by being more compressed antero-posteriorly. In M^3 the paracone is slightly smaller than the metacone, but larger than the protocone. The metacone is directly posterior to the paracone, both cusps lying slightly external to the longitudinal midline. The paracone and metacone are crested externally, giving both cusps a strong V-shaped appearance: the postero-external paracone crest and the antero-external metacone crest meet on the antero-posterior midline; the sharp antero-external paracone

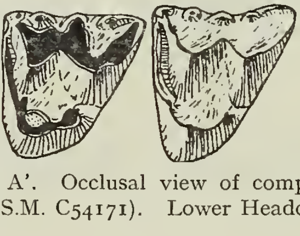

FIG. 11. '*Peratherium* species A'. Occlusal view of composite left M^2–M^3 ×10. M^2 (S.M. C54170) and M^3 (S.M. C54171). Lower Headon Beds, Hordle Cliff.

crest meets the antero-external stylar cusp and the postero-external metacone crest forms the sharp postero-external tooth margin. From the antero-internal protocone a crest runs antero-externally, dilating into a small but distinct paraconule just internal to the paracone base; the crest continues antero-externally as a cingular shelf at the base of the anterior wall of the paraconid. A similar crest runs from the protocone, swelling into a metaconule just internal to the metacone base; the metaconule is larger than the paraconule.

There are four well-developed rounded stylar cusps on the external cingular margin: stylar cusp A on the antero-external extremity of the tooth is joined to the antero-external paracone crest; the larger more elongated stylar cusp B is well separated from cusp A; stylar cusp C, subequal with cusp B, lies on the transverse midline of the tooth; stylar cusp D, smaller and less distinct than C, continues as a small crest to the postero-external extremity of the tooth. Stylar cusp E is absent. The external margin is slightly embayed in the region of stylar cusp C. The area between protocone, metacone and paracone is strongly basined, and to a lesser extent, between the metacone/paracone and the external stylar cusps.

M^2 is similar to M^3 but there are several minor differences: the tooth is slightly longer antero-posteriorly; the metacone is more markedly larger than the paracone; the paracone and metacone are subequal; the conules are stronger, the metaconule giving the tooth a more blunted appearance internally, and stylar cusp A is smaller and cusp B larger, although cusp C is still larger than cusp D.

REMARKS. The bulk of the material is from the Lower Headon Beds of Hordle Cliff. The exact horizon and locality are unknown, but a coarse white sand matrix on some specimens indicates possible derivation from the Crocodile Bed. Two specimens from the Isle of Wight extend the species range into the Upper Headon Beds. The isolated upper molars are referred to this species because of similar dimensions and good occlusion with the lower molars.

There is little variation in the teeth dimensions in this material. S.M. C53476 and S.M. C30707 have much deeper mandibles but also more wear on the teeth,

TABLE 5

Measurements (in mm) of '*Peratherium* species A'

	P_2		P_3		M_1		M_2		M_3		M_4	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30350	—	—	—	—	—	—	1·7	1·2	1·9	1·1	1·8	1·0
F.C.S. 2	—	—	—	—	—	—	—	—	1·95	1·3	—	—
B.M. M26050	—	—	—	—	—	—	—	—	2·0	1·3	—	—
S.M. C30707	1·3	0·7	1·5	0·75	1·6	1·1	1·7	1·2	1·7	1·1	—	1·0
S.M. C53476	—	—	—	—	—	—	1·6	1·35	1·8	1·3	—	—
S.M. C30708	—	—	—	—	—	—	—	—	1·85	1·05	—	—
B.M. 36812b	—	—	—	—	—	—	—	—	—	—	1·8	0·9
B.M. 30348	—	—	—	—	—	—	—	—	1·9	1·2	1·8	1·0

	M^2		M^3	
	a-p	trs	a-p	trs
S.M. C54171	—	—	1·8	2·0
S.M. C54170	1·95	2·0	—	—

which may indicate a greater individual age. Hough observed (1961), that in recent didelphids, spaces tend to appear between the premolars in the mature adult. This feature of the premolars in S.M. C30707, may be similarly a variation due to individual age.

'*Peratherium* species B'

(Text-fig. 12)

Material. All specimens, except where otherwise stated, are from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 13250 (2). Fragment of left mandibular ramus with M_2–M_4 and the basal part of the coronoid. Teeth badly worn.

B.M. M13251. Fragment of left mandibular ramus with M_2–M_4 and alveoli of C–P_3 and M_1. Teeth badly worn.

B.M. 13250 (3). Fragment of right mandibular ramus with M_3–M_4. Teeth badly worn.

S.M. C54155. Fragment of left mandibular ramus with M_1–M_2 and alveoli of M_3. Teeth badly worn. Lower Headon Beds, Hordle Cliff. The Sedgwick Museum label gives 'Rodent Bed' as the locality but the preservation and adhering white sand suggests probable derivation from the Mammal/Crocodile Bed.

S.M. C53474. Anterior fragment of left mandibular ramus with M_2 and alveoli of the canine (base), P_1–M_1 and M_3. Teeth moderately worn.

B.M. 44142 (1). Fragment of right mandibular ramus lacking teeth, with alveoli of P_1–M_4.

(2). Small fragment of right mandibular ramus with alveoli of uncertain position in the tooth row.

S.M. C53480. Fragment of right mandibular ramus with posterior root of M_2 and the roots of M_3–M_4.

S.M. C54169. Isolated trigonid fragment of left lower molar. Badly worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

Description. The posterior mental foramen lies below M_1 (B.M. M13251) or M_2 (S.M. C53474); the anterior mental foramen is situated below P_1 (B.M. M13251) or P_2 (S.M. C53474). The subhorizontal symphysial surface extends to below P_2. S.M. C53474 possesses a nutrient foramen (as in S.M. C30707, referred to '*Peratherium* species A') opening through the symphysial surface.

No description is given of the dentition which is structurally almost identical to previously described specimens referred to '*Peratherium* species A'.

Remarks. Because of the much larger dimensions of the teeth (especially the length of the tooth row) compared with '*Peratherium* species A', these specimens are considered to represent a distinct species. Hough stated (1961), that this criterion is less subject to variation than depth of mandible and spacing of premolars, and has been used in the determination of *Marmosa* species. There is some variation in mandible depth and premolar spacing; as in '*Peratherium* species A' this probably reflects individual age differences.

Two mandibular fragments without teeth (B.M. 44142 (2) and S.M. C53480) are tentatively referred to this species. B.M. 44142 (1) is considerably longer and more slender than the other referred specimens with widely spaced anterior premolars; it is considered tentatively as an old adult of '*Peratherium* species B'.

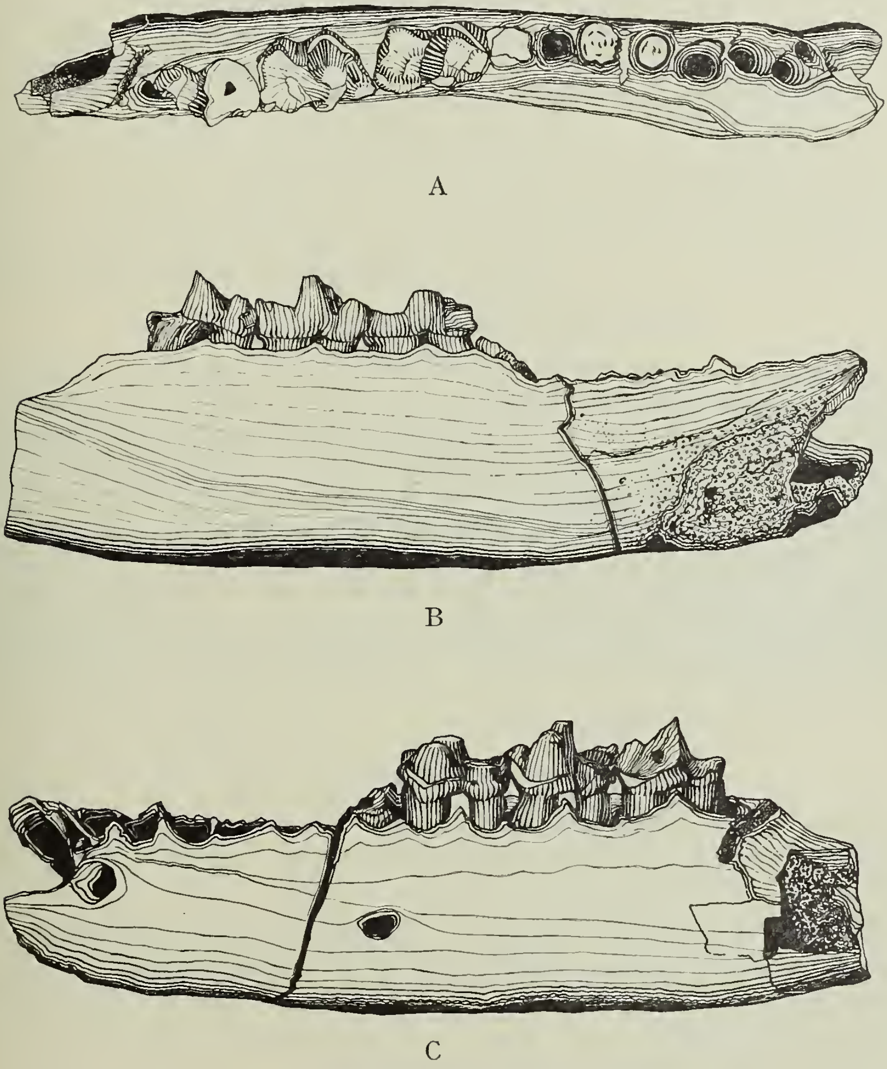

Fig. 12. '*Peratherium* species B'. Fragmentary left mandibular ramus with M_2–M_4. B.M. M13251 ×6. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

A pathological condition is seen in S.M. C53480. The mandible evidently had been damaged during life internally below M_2 and M_3, and shows some formation of callus in this area.

TABLE 6

Measurements (in mm) of '*Peratherium* species B'

	M_1		M_2		M_3		M_4	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 13250 (2)	—	—	2·5	1·75	2·5	1·6	2·5	1·4
B.M. M13251	—	—	2·5	1·6	2·55	1·6	2·25	1·4
B.M. 13250 (3)	—	—	—	—	2·5	1·5	2·5	1·35
S.M. C53474	—	—	2·6	1·4	—	—	—	—
S.M. C54155	2·7	1·4	2·7	1·7	—	—	—	—

Order INSECTIVORA

Family **NYCTITHERIIDAE** Simpson, 1928

REMARKS. Simpson's family Nyctitheriidae was abandoned by McKenna (1960a) as an unnatural unit. Van Valen (1967) placed *Nyctitherium* together with *Clinopternodus* Clark, 1937, as a subfamily (Nyctitheriinae) within the Adapisoricidae. On the basis of Robinson's (then unpublished) work on the group, McKenna (1968) recognised 'a restricted family-group taxon based on *Nyctitherium* and several referred genera', into which he placed *Leptacodon*. In his review of the family, Robinson (1968) upheld the status of Simpson's family Nyctitheriidae, subdividing it into three subfamilies: Nyctitheriinae Simpson, 1928; Geolabidinae McKenna, 1960; and Micropternodontinae (Stirton & Rensberger, 1964). The Geolabidinae, placed originally by McKenna (1960b) in the Erinaceidae, had been grouped by Van Valen (1967) within the Adapisoricidae. Robinson's view is adopted here.

Subfamily **NYCTITHERIINAE** Simpson, 1928

DIAGNOSIS. P_4^4 semi-molariform, P_2, P_3 with two roots each, P_1 with one root, jaw long and slender, with no apparent shortening. Probable dental formula $\frac{?}{3}, \frac{?}{1}, \frac{4}{4}, \frac{3}{3}$. (Robinson, 1968 : 129).

REMARKS. Three genera were included by Robinson (1968) in the subfamily:

Nyctitherium Marsh, 1872. Middle—Late Eocene; North America.

Leptacodon Matthew & Granger, 1921. Middle (?), Late Palaeocene—Early Eocene; North America.

Saturninia Stehlin, 1940. Late Eocene; Europe.

To these are added two new genera described below.

Leptacodon has undergone a varied history. McKenna (1960a : 52 and 1960b : 156) removed *Leptacodon* (*sensu stricto*) from the Leptictidae; this genus, composed of *L.*

tener Matthew & Granger, 1921 (the type species); *L. ladae* Simpson, 1935 (apparently, but not mentioned specifically by McKenna); *L. minutus* Jepsen, 1930, and *L. jepseni* McKenna, 1960a, was considered to be near the base of erinaceid phylogeny and possibly closely related to the ancestry of the Geolabidinae. This tentative reference of *Leptacodon* (*sensu stricto*) to the Geolabidinae was accepted by Russell (1964 : 46). Van Valen (1967) placed *Leptacodon* (*sensu stricto*) in the Adapisoricidae (subfamily Adapisoricinae) and more recently, McKenna (1968) has stated that the genus is perhaps best considered as a nyctithere. Robinson (1968) in his review of the Nyctitheriidae, clarified the systematics of the genus *Nyctitherium;* he indicated that the type specimen of *Myolestes dasypelix* Matthew, 1909, is a nyctitherine, although he has agreed with McKenna's allocation of a referred specimen 'c.f. *Myolestes dasypelix*' to the Geolabidinae (McKenna, 1960b : 147). In addition to *Nyctitherium dasypelix*, Robinson (1968) recognised two further species: the type species, *N. velox* Marsh, 1872, and *N. serotinum* (Marsh, 1872). In the same paper, he rejected Stehlin's reference of *Saturninia* to the Soricidae, maintaining for the genus, a close relationship with *Nyctitherium.*

Genus ***SCRAEVA*** gen. nov.

ETYMOLOGY. Screawa—(Anglo-Saxon), a shrew.

DIAGNOSIS. In P_4–M_3, talonid narrower transversely than trigonid; talonid and trigonid subequal in length; trigonid with markedly angular outline, with straight or slightly convex internal margin and moderately to sharply pointed anterior apex; protoconid larger than metaconid; talonid angular with internal and external margins subparallel, except on M_3. M_1–M_3 with a mesoconid; hypoconid and entoconid subequal in size; hypoconulid median or slightly internal of midline, in M_3 posteriorly projecting as a prominent rounded lobe. P_4 hypoconulid minute, slightly external to midline. Internal face of coronoid process with antero-posterior ridge at molar alveoli level.

TYPE SPECIES. *Scraeva hatherwoodensis* sp. nov. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

REMARKS. One other species has been distinguished: *Scraeva woodi* sp. nov. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

In 1844, Charlesworth (*in* Wood, 1844 : 350, footnote) recorded a fragmentary mandibular ramus, obtained by Flower from Hordle Cliff, which he named *Spalacodon;* this was again recorded by Charlesworth (1845 : 50). A year later, the specimen was figured by Wood (1846, pl. 2, figs 5, 5a-c) and listed as 'an imperfect lower jaw'. Charlesworth and Wood did not designate a species and the specimen was referred to as '*Spalacodon*' or '*Spalacodon* sp.' Because of the inadequate original descriptions and the loss of the specimen, *Spalacodon* is considered here to be a *nomen nudum.* Comparison of the type material of *Scraeva woodi* with Wood's illustrations indicate the probable specific identity of the two forms. This contention is strengthened by the probability that *Spalacodon* and the material of *Scraeva woodi* were obtained from the same level, the Crocodile Bed of Hordle Cliff. The specimen described by

Charlesworth and Wood (from Wood's figures, a right mandibular ramus with P_2 and P_4–M_3) has not been located during the present study and the material is considered to be lost.

Scraeva is referred to the Nyctitheriidae mainly on the basis of strong resemblances to *Leptacodon* and *Nyctitherium*. The soricid-like antero-posterior internal ridge on the coronoid, characteristic of *Nyctitherium* (Robinson, 1968), is well developed in *Scraeva*. A talpid characteristic, occasionally developed in *Nyctitherium* and present also in *Saturninia*, is a continuation of the crista obliqua up the posterior wall of the metaconid; this is prominently and invariably developed in *Scraeva*. The Headon genus is distinguished from other nyctitheres as follows: In *Nyctitherium* (see Robinson, 1968), P_4 has a smaller talonid basin and lacks an entoconid; in the molars, the hypoconulid is more internal in position and smaller and the paraconid is more internally situated. In this study the type specimen of *Saturninia* has not been examined, but from Stehlin's illustrations (1940, fig. 1c, fig. 2c) the P_4 is relatively smaller with a less basined talonid, and the molar paraconids are more internal in position. In addition, in both *Nyctitherium* and *Saturninia*, the outline of P_4–M_3 is more rounded and the P_4–M_3 trigonid and talonid are of similar transverse width.

The P_4 of *Scraeva* is very similar to that of the type species of *Leptacodon*, *L. tener*, except for a rounded posterior talonid margin and a sharper, more separated paraconid in *Leptacodon tener*. The molars are also similar although in *Leptacodon tener*, the metaconid is as high as the protoconid; the paraconid is somewhat sharper and more separated; the M_3 hypoconulid is less projecting posteriorly and the trigonid cusps are not so elevated above the talonid. Less resemblance is apparent in the P_4 of *Leptacodon ladae* which has a more isolated median paraconid, a more anteriorly placed protoconid and a much shorter talonid.

Scraeva also shows marked resemblances to *Scenopagus* McKenna & Simpson, 1959, *Messelina* Tobien, 1962, and *Adapisorex* Lemoine, 1883; these genera have been generally regarded as 'primitive probable erinaceids', although extensive regrouping and familial separation from the Erinaceidae has been proposed by Van Valen (1967 : 261). In several respects, particularly the elevated trigonids and the structure of M_3, *Scraeva* is similar to *Scenopagus* but there are significant differences: in *Scenopagus*, the talonid cusps of the molars are slightly higher; the trigonid cusps are compressed antero-posteriorly and the paraconid crest is larger and more oblique, resulting in a blunter anterior tooth apex; the hypoconid crest runs to the internal base of the protoconid, not the metaconid as in *Scraeva*, and the hypoconulid is only slightly developed in M_1–M_2. P_4 has not been adequately described or figured. In *Messelina*, the lower molars are much narrower transversely; the talonid and trigonid are subequal in width and the hypoconulid is internal; the trigonid of the molars is not elevated, and in M_1–M_2 the trigonid and talonid cusps are subequal in height. Also, the P_4 of *Messelina* has a rounded outline and lacks a hypoconulid. Greater resemblance to *Scraeva* is seen in *Adapisorex:* in the molars of both genera, the protoconid is larger than the metaconid (but not so extremely developed in *Scraeva*) and the basined talonid has a median hypoconulid. The P_4 is similar in *Scraeva* and *Adapisorex*, with a small metaconid, a large protoconid anterior to the metaconid which dominates the trigonid (less extremely so in *Scraeva*) and a small median hypoconulid. However, *Adapisorex* is distinguished from *Scraeva* by having much lower-placed cusps, the trigonid being little elevated above the talonid; the entoconid and hypoconid are much larger and the trigonid and talonid are subequal in width.

In basic structure, particularly of P_4–M_2, *Adunator* Russell, 1964 (originally considered by Russell as a leptictid but placed by Van Valen, 1967, in the Adapisoricinae) shows similarities to *Scraeva*, although the P_4 paraconid is much more separated anteriorly as a distinct cusp. Also, in *Adunator* the M_3 hypoconulid is more internal and not so projecting as an isolated lobe, and in the molars the metaconid and entoconid are higher than the protoconid and hypoconid respectively.

Scraeva hatherwoodensis sp. nov.

(Text-fig. 13)

Etymology. hatherwoodensis—from Hatherwood Point, off Headon Hill, Isle of Wight, the sea cliff locality.

Diagnosis. The smaller species. P_4–M_2 trigonid with a slight posterior tilt. P_4–M_2 with straight internal trigonid margin and protoconid and metaconid more internally placed than in *S. woodi*. P_4 metaconid and protoconid slightly lower than corresponding cusps of M_1; paraconid median, at same height as molar paraconids. P_4 metaconid more posteriorly placed in relation to protoconid than in *S. woodi*, in M_1 metaconid only slightly posterior to protoconid.

Holotype. B.M. M26051. Fragment of left mandibular ramus with P_4–M_2 and alveoli of I_3–P_3 and M_3. Lower external surface embedded in matrix. Teeth slightly worn. Upper Headon Beds (*Microchoerus* Bed), Headon Hill. The only specimen of the species.

Description. The long slender mandible has a large oval posterior mental foramen just below the alveolar level of P_3. There is a small angular process (tip damaged on the specimen) at molar alveoli level. The coronoid and condyle are not preserved. The mandibular foramen is visible just below alveolar level. On the internal face of the coronoid, a prominent antero-posterior ridge runs from the level of the M_3 alveoli towards the mandibular foramen. A similar ridge was observed by Simpson (*in* McGrew, 1959) on a toothless mandibular fragment from the Middle Eocene of Wyoming, tentatively referred to the Soricidae. This structure also occurs in *Nyctitherium* (Robinson, 1968 : 130).

M_3 is double-rooted and known only by alveoli. In M_1–M_2 the talonid and trigonid are subequal in length, but the talonid is narrower transversely. The internal and external talonid margins are straight and subparallel. The trigonid is angular with a sharp anterior apex and a straight internal margin; sharply elevated, it falls almost vertically to a low basined talonid. There is a prominent antero-external cingulum.

The protoconid is larger than the metaconid and slightly more anteriorly placed (on both M_1 and M_2 the metaconid is damaged). The paraconid is moderately well separated and cuspate, forming the sharp anterior extremity of the trigonid; this cusp is median in M_1 but slightly internal to this position in M_2. The hypoconid and entoconid are subequal; the hypoconulid is a little smaller but comparison is difficult as the entoconid is almost unworn, whereas the hypoconid and hypoconulid are badly worn. The median hypoconulid (in M_2 slightly internal to the midline) is posterior to the hypoconid and entoconid, projecting very slightly posteriorly and joined to the hypoconid and entoconid by small low crests. From the entoconid a low feeble crest runs anteriorly to the metaconid base. A stronger crista obliqua runs from the hypoconid up the posterior wall of the metaconid; this crest swells into a prominent mesoconid (stronger on M_1 than M_2) midway along its length.

P_4 is very similar to M_1 and M_2 but differs in several respects: the tooth is more laterally compressed and smaller in all dimensions; the hypoconulid is very small, situated external to the midline near the hypoconid; the metaconid is more posterior in relation to the protoconid; the hypoconid is larger than the entoconid and the protoconid/paraconid crest is smaller, placed slightly external to the midline and less V-shaped than in the molars. P_3 and P_2 are represented only by alveoli; these teeth were apparently double-rooted and closely spaced. P_1 is single-rooted, represented only by the alveolus. Known only from the alveolus, the canine was evidently slightly anteriorly inclined, with a root diameter as that of P_1. I_3 is represented by the possible base of the alveolus.

REMARKS. This species is clearly related to *Scraeva woodi* in that both forms exhibit the characteristic squared angular outlines of the teeth. There are a number of small but distinct differences between *S. hatherwoodensis* and *S. woodi* (see diagnoses) which indicate at least a specific separation. Also, *S. woodi* is markedly larger.

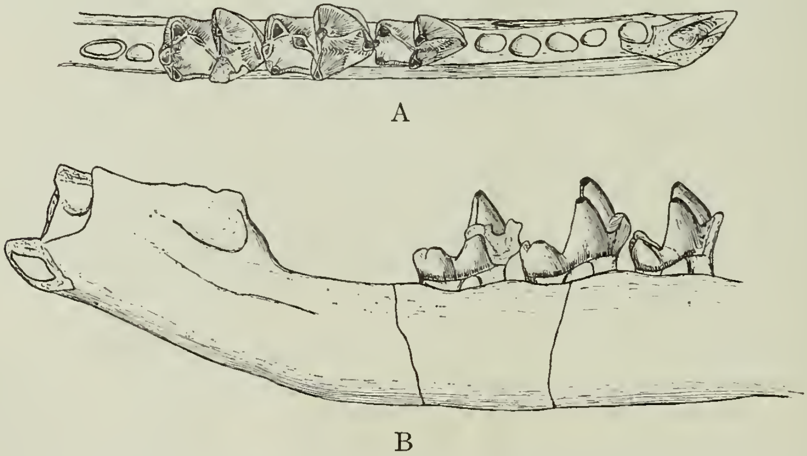

Fig. 13. *Scraeva hatherwoodensis* gen. et sp. nov. Fragmentary left mandibular ramus with P_4–M_2. Holotype (B.M. M26051) × 10. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) Internal view.

TABLE 7

Measurements (in mm) of *Scraeva hatherwoodensis*

	P_4		M_1		M_2	
	a-p	trs	a-p	trs	a-p	trs
Holotype (B.M. M26051)	1·35	0·9	1·5	1·1	1·5	1·2

Scraeva woodi sp. nov.

(Text-fig. 14)

ETYMOLOGY. woodi—after Searles Wood who first listed and figured insectivore material from the Headon Beds as *Spalacodon*, a name suggested by Charlesworth, but here considered as a *nomen nudem.*

DIAGNOSIS. Larger than *S. hatherwoodensis.* P_4 with slightly concave internal trigonid margin, in molars slightly convex. P_4 metaconid and protoconid same height as corresponding cusps of M_1; paraconid markedly internal, lower than molar paraconids. P_4 metaconid slightly posteriorly placed in relation to protoconid, in M_1 metaconid opposite and in M_2–M_3 metaconid slightly anterior to protoconid.

HOLOTYPE. S.M. C53475. Fragment of left mandibular ramus with P_4–M_3 and alveoli of P_3. Teeth unworn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

PARATYPE. B.M. M25112. Left mandibular ramus with P_2, P_4–M_3 and alveoli of I_2–P_1, P_3. Badly worn dentition. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

MATERIAL. S.M. C30709. Fragment of left mandibular ramus with M_1–M_2, posterior alveolus of P_4, and alveoli of M_3. Teeth unworn but metaconids damaged. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 36801c. Fragment of left mandibular ramus with M_2 and alveoli of M_3 Internal margin of tooth damaged and tips of cusps broken off. Patches of coarse white sand matrix adhering. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

S.M. C54168. Isolated right M_2. Slightly worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The mandible is a little stouter than in *S. hatherwoodensis*, with a large oval posterior mental foramen below the posterior root of P_3. The antero-posterior ridge on the internal face of the coronoid is present as in *S. hatherwoodensis.* Paratype B.M. M25112 shows the wedge-shaped symphysial surface with ridged margins; this occupies nearly the whole depth of the jaw under I_2, sloping baso-posteriorly to below the anterior root of P_2.

The incisors, canine and P_1 are known only from alveoli in paratype B.M. M25112. In this specimen, two distinct, well-separated alveoli both slightly smaller than the P_1 alveolus, indicate at least two incisors, here considered as I_2–I_3. Another more anterior tooth may have been present but evidence is lacking. The canine is represented by an alveolus indicating a larger anteriorly-inclined tooth. P_1, single-rooted and well-separated, is represented by the alveolus which is smaller than that of the canine. P_2 is double-rooted and oval in outline. A single large anterior median cusp slopes antero-basally to a small low antero-internal cuspule; a small heel bears a minute internal cuspule. P_3 is known only from the alveoli; the tooth is double-rooted and apparently about the same size as P_2.

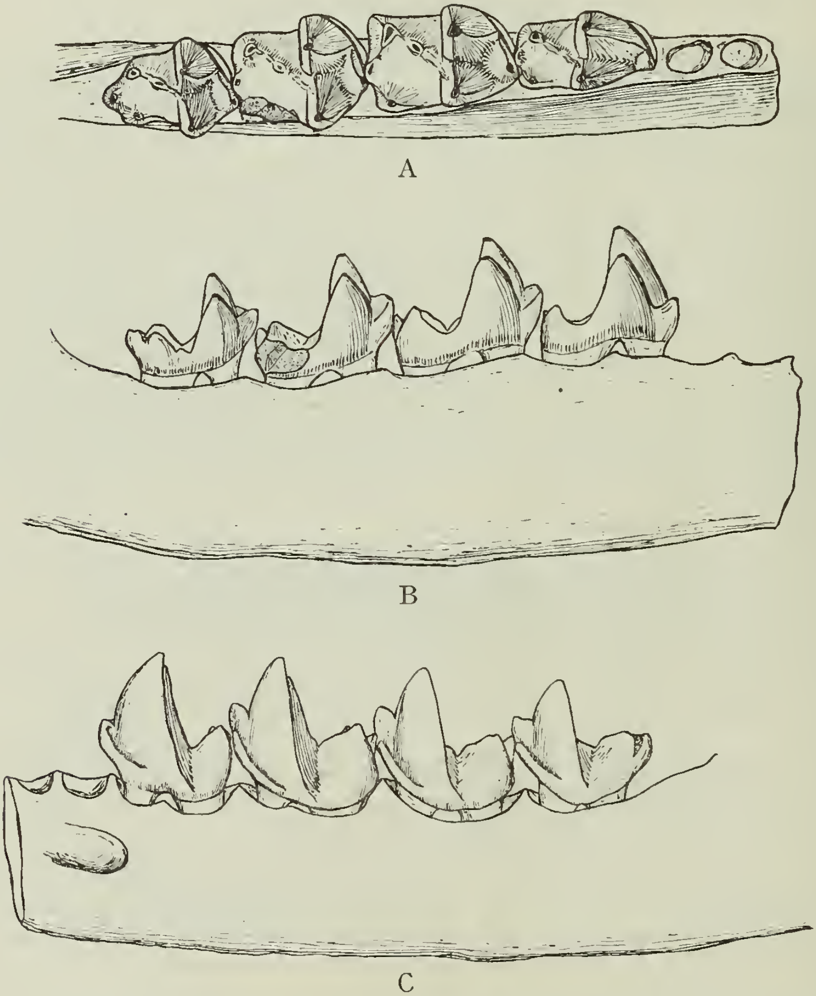

FIG. 14. *Scraeva woodi* gen. et sp. nov. Fragmentary left mandibular ramus with P_4–M_3. Holotype (S.M. C53475) × 10. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

The trigonid and talonid in P_4 are subequal in length. In M_1–M_3 the talonid is slightly more elongated antero-posteriorly and narrower transversely; the internal and external margins are fairly straight and subparallel, except in M_3 where the talonid narrows posteriorly (not as extreme as in *S hatherwoodensis*). The M_2 in paratype B.M. M25112 has a somewhat indented external margin. P_4 and M_3 are narrower transversely than M_1 and M_2. In P_4–M_3 the trigonid is angular with only a slightly curved internal margin; sharply elevated, it drops steeply to a low basined talonid. There is a prominent antero-external cingulum as in *S. hatherwoodensis.* The metaconid is smaller than the protoconid, situated posterior to the protoconid in P_4, opposite in M_1 and slightly anterior in M_2 and M_3. The paraconid, moderately well separated and cuspate, forms the fairly sharp antero-internal extremity of the tooth—this cusp is moderately internal to the midline in all teeth (P_4–M_3). The hypoconulid in M_1 and M_2 is a little smaller than the entoconid and median in position; in P_4, it is very small and slightly external to the midline (but in M_3, hypoconulid, entoconid and hypoconid are subequal). The P_4 hypoconulid in paratype B.M. M25112 is indistinct, indicated only by a slight externally situated projection posterior to the hypoconid and entoconid. M_3 has a posteriorly projecting hypoconulid lobe, slightly internal to the midline; this lobe is very prominent and apically projecting in paratype B.M. M25112. In P_4–M_3 the hypoconulid is joined to the hypoconid and entoconid by small low crests; a low feeble crest runs antero-internally from the entoconid to the metaconid base. A much stronger crista obliqua runs from the hypoconid up the posterior wall of the metaconid; this crest bears a distinct mesoconid in M_1–M_3, although the cusp is only feebly developed in M_2.

REMARKS. Comparison with *S. hatherwoodensis* has been effected in the diagnosis and description. Only five specimens are known and little idea can be gained of variation within the species. S.M. C30709 and S.M. C54168 differ from the holotype only by having a less distinct mesoconid in the molars. Paratype B.M. M25112 represents a much older individual than the holotype and comparison of the two specimens is difficult because of a high degree of wear on the former specimen. Reference of B.M. M25112 to the species is fairly certain, however; when structural differences which can be assigned to excessive wear are discounted, the two specimens have a high degree of similarity. Also, both specimens are apparently from the same locality and approximate horizon. B.M. 36801c appears closely similar to the holotype, although the former specimen is damaged.

TABLE 8

Measurements (in mm) of *Scraeva woodi*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. M25112	1·45	0·6	—	—	1·7	1·05	1·75	1·45	1·8	1·45	1·8	1·2
B.M. 36801c	—	—	—	—	—	—	—	—	1·7	1·15	—	—
S.M. C54168	—	—	—	—	—	—	—	—	1·8	1·25	—	—
S.M. C53475	—	—	—	—	1·6	1·0	1·95	1·3	1·85	1·4	1·8	1·2
S.M. C30709	—	—	—	—	—	—	1·8	1·15	1·7	1·25	—	—

Genus ***ARVALDUS*** gen. nov.

ETYMOLOGY. Arvaldus—Jutian king of the Isle of Wight, A.D. 686.

DIAGNOSIS. P_4 protoconid markedly anterior to the metaconid; hypoconulid (damaged) appears more prominent than in *Scraeva*. P_4–M_3 posterior margin somewhat oblique to length of tooth row; paraconid internal; protoconid larger than metaconid; P_4 hypoconid opposite, M_1–M_2 slightly posterior, and in M_3 markedly posterior to entoconid. M_3 hypoconulid prominent, internal to midline, slightly projecting; talonid angular in outline with straight posterior and postero-internal margins.

TYPE SPECIES. *Arvaldus stintoni* sp. nov. Upper Headon Beds (Lignite Bed), Headon Hill. The only known species.

REMARKS. *Arvaldus* shows considerable similarity with *Leptacodon, Nyctitherium* and *Saturninia*. The P_4 of *Leptacodon tener* (the type species) seems quite close to that of *Arvaldus* with a well differentiated talonid and the protoconid strongly anterior to the metaconid, although in P_4 of *L. tener*, a hypoconulid is absent and the posterior talonid margin has a rounded outline. Similarity with the P_4 of *Leptacodon ladae* is shown by the anterior position of the protoconid and the presence of a small hypoconulid, although in several other respects—the median paraconid, rounded outline and small talonid, the tooth is rather different. The type species of *Nyctitherium, N. velox,* is distinguished from *Arvaldus* by the P_4 talonid being much shorter antero-posteriorly with the protoconid opposite the metaconid; in the molars, the paraconid is more internal and the hypoconulid is weaker and placed more internally, although in this latter respect, *Arvaldus* is closer to *N. serotinum* where the molar hypoconulid is slightly more median in position. In *Saturninia* the P_4 protoconid is opposite the metaconid and the paraconid of the molars is more internally situated.

One of the most obvious features which distinguishes *Leptacodon, Nyctitherium, Saturninia* and *Scraeva* from *Arvaldus* is the structure of M_3. In *Leptacodon* there is a strong entoconid opposite the hypoconid and a well separated posteriorly projecting hypoconulid. This tooth in *Nyctitherium velox* is different in outline; the talonid is shorter with a median hypoconulid and an entoconid which is opposite the hypoconid. The M_3 talonid in *Saturninia* is shorter and different in outline with a median posteriorly projecting hypoconulid. In M_3 of *Scraeva* the entoconid and hypoconid are opposite and there is a median posteriorly projecting hypoconulid.

In this M_3 talonid structure, *Arvaldus* shows similarities with the American geolabidines, *Geolabis*, 'c.f. *Myolestes dasypelix*' and *Centetodon*, particularly the latter. In *Centetodon*, the M_3 talonid bears only a hypoconid and an internal crestiiform hypoconulid (fused entoconid and hypoconulid?); the internal wall of the postero-internally projecting hypoconulid curves abruptly baso-posteriorly and there is no sign of an entoconid. A somewhat similar distinctive M_3 talonid structure is seen in *Arvaldus*, although here it is not so pronounced; the hypoconulid is less posteriorly situated and a small anteriorly placed entoconid is still present. However, in *Centetodon* and other geolabidines, the structure of P_4 is different: in the American forms, the P_4 protoconid and metaconid are opposite and the talonid is much reduced, with a single large internal cusp. Greater similarity to *Arvaldus* is seen in the P_4 of 'c.f. *Hypacodon* sp.' (= *Centetodon* sp.) described by McKenna (1960b : 150). Here the elongation of the tooth is similar to that in *Arvaldus* and the protoconid is anterior to the metaconid; the talonid is more developed and there is a central hypoconid and a small though distinct entoconid. Robinson (1968 : 134) has considered this specimen as an adapisoricid.

Arvaldus differs from *Scraeva* in a number of important aspects (see diagnoses), the more obvious of these being the non-angular tooth outlines, the structure of P_4 and the distinctive M_3 talonid; the two genera do not appear to be closely related. To some extent, the structure of *Arvaldus* is intermediate between nyctitherines and geolabidines and on the basis of the M_3 structure, the genus could be regarded as a primitive relatively unspecialised geolabidine. However, the molarised P_4 and the continuation of the crista obliqua up the posterior wall of the metaconid support reference to the Nyctitheriinae. The anterior lower dentition and the upper teeth of *Arvaldus* are unknown. At present the European record of the family comprises *Saturninia*, *Scraeva* and *Arvaldus*, all from the Upper Eocene. It is likely that the phyletic position of *Arvaldus* will be clarified with the discovery of nyctitheriids from the Lower Eocene of Europe.

Arvaldus stintoni gen. et sp. nov.

(Text-fig. 15)

ETYMOLOGY. stintoni—after Mr F. C. Stinton, the finder of the specimen.

DIAGNOSIS. No other species are known and the diagnosis is the same as that for the genus.

HOLOTYPE. F.C.S.I. Fragment of right mandibular ramus with P_2, P_4–M_3 and the alveoli of P_3. Upper Headon Beds (Lignite Bed), Headon Hill. The only known specimen of the species.

DESCRIPTION. The mandible has a large posterior mental foramen below P_3. The posterior region is not preserved. P_2 is very similar to that of the paratype of *Scraeva woodi* (B.M. M25112). The tooth is double-rooted and oval in outline with a large median anterior cusp, which slopes baso-anteriorly to a small low antero-external cuspule. A small low heel bears a single minute internal cuspule. Represented by only alveoli, P_3 is double-rooted and apparently a little smaller than P_2.

In P_4–M_3, the talonid is a little longer antero-posteriorly than the trigonid especially in M_3 and about the same width, with an indented internal and external margin. The trigonid has a curved internal margin. The posterior wall drops less steeply than in *Scraeva*. There is a prominent antero-external cingulum. The protoconid is larger than the metaconid and situated opposite to it in M_1–M_3; in P_4 the protoconid is markedly anterior to the metaconid. The cuspate paraconid is moderately well separated and situated internally in all four teeth as in *Scraeva woodi*. The P_4 paraconid is sharper and more anteriorly projecting than in this latter species. In P_4–M_3 the hypoconid is stouter than the entoconid; the hypoconulid is a little smaller than the entoconid or subequal, except on M_3 where it is a little larger; this cusp is slightly external to the midline in P_4, median in M_1 and slightly internal in M_2 and M_3; it is posterior to the entoconid and hypoconid and projecting slightly in all four teeth. The hypoconulid is well separated from the entoconid but is joined to the hypoconid by a small low external crest. In P_4, the hypoconid is opposite to the entoconid, in M_1 and M_2 slightly posterior and in M_3 markedly posterior. From the entoconid, a feeble crest runs antero-internally to the base of the metaconid. A stronger crista oblique runs antero-internally from the hypoconid up the posterior wall of the metaconid; this swells up midway along its length into a prominent mesoconid. The enclosed talonid is deeply basined. The posterior margin of the talonid is slightly obliqua to the length of the tooth in P_4–M_2 (a tendency also seen in paratype B.M. M25112 of *Scraeva woodi*). In M_3 the straight posterior margin runs from the sharp postero-external extremity of the talonid to the slightly more posteriorly situated hypoconulid. From this latter cusp, the straight talonid margin runs obliquely forwards to the relatively anteriorly-placed entoconid.

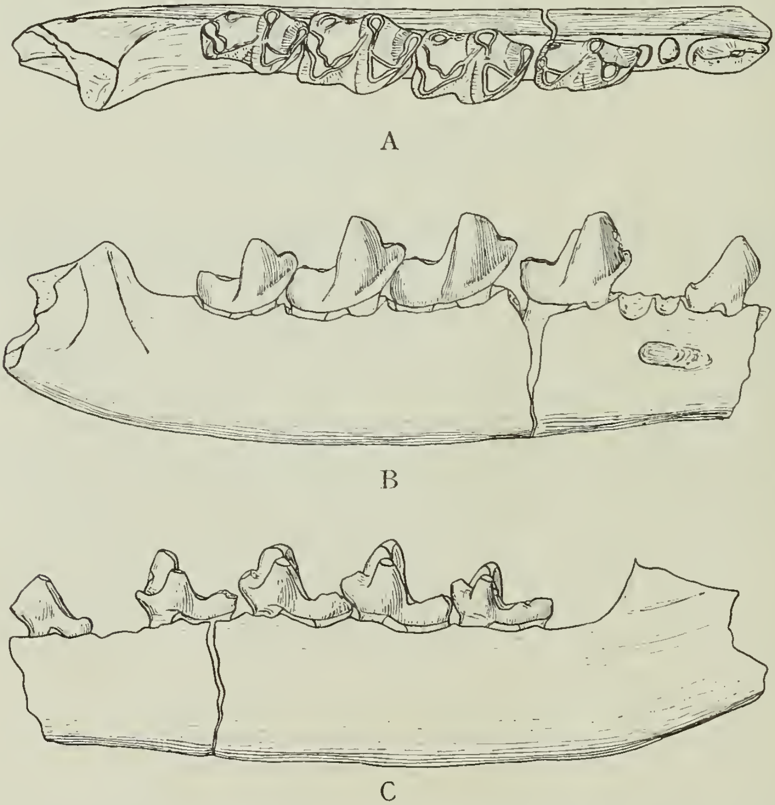

FIG. 15. *Arvaldus stintoni* gen. et sp. nov. Fragmentary right mandibular ramus with P_2, P_4–M_3. Holotype (F.C.S. 1) ×10. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) External view. (C) Internal view.

TABLE 9

Measurements (in mm) of *Arvaldus stintoni*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
Holotype (F.C.S. 1)	1·2	0·5	—	—	1·5	0·8	1·6	1·1	1·65	1·2	1·5	0·9

Family **PANTOLESTIDAE** Cope, 1884

DIAGNOSIS. Facial part of skull short, basicranial region broad, middle portion of skull elongate. Angle of mandible a short stout process expanded at the tip. Mental foramen usually beneath M_1, sometimes below P_4. Dental formula $\frac{3}{?}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$. Molars and premolars with low massive cusps. Canines large, massive, lower canines often semiprocumbent. Upper incisors spaced and peg-like. P_1–P_3 elongate and fairly small. P_4 relatively enlarged (after Matthew, 1909).

REMARKS. On the basis mainly of differences in the structure of P^4_4, two subfamilies have been traditionally distinguished:

Pantolestinae Simpson, 1937
Pentacodontinae Simpson, 1937

Gazin (1959) erected a new subfamily, Apheliscinae; this was referred by McKenna (1960a) to the condylarths (Hyopsodontidae). Van Valen (1966) supported Gazin's reference of the Aphelescinae to the Pantolestidae, but more recently (1967) has agreed with McKenna's removal of the group to the Hyopsodontidae.

Van Valen (1967) in his revision of insectivore classification raised the pentacodonts to family level. As the justification for such a procedure (Van Valen, 1967 : 321) seems no greater than that for retaining them in the Pantolestidae, the old-established two fold subdivision of the Pantolestidae is retained here.

Subfamily **PANTOLESTINAE** Simpson, 1937

DIAGNOSIS. P^4_4 relatively little enlarged. P_4 compressed, no metaconid, semi-shearing, heel essentially unicuspid and little or not basined. P^4 with compressed amphicone, no metacone, low, sharp styles, small protocone without cingula (Simpson, 1937).

REMARKS. The Pentacodontinae are distinguishable from this subfamily by P^4_4 being much enlarged; P_4 has a well developed metaconid and basined talonid; P^4 has a distinct metacone, large protocone, with expanded cingula and styles are small or absent.

The following genera have been referred, to date, to the Pantolestinae:

Propalaeosinopa Simpson, 1927. Middle-Late Palaeocene; North America.
Bessoecetor Simpson, 1936. Middle-Late Palaeocene; North America. ?Late Palaeocene; Europe.
Pagonomus Russell, 1964. Middle-Late Palaeocene, ?Early Eocene; Europe.
Pantomimus Van Valen, 1967. Middle Palaeocene; North America.
Palaeosinopa Matthew, 1901. Late Palaeocene-Early Eocene; North America.
Pantolestes Cope, 1872. Middle Eocene; North America.
Cryptopithecus Schlosser, 1890. Late Eocene; Germany.
Opsiclaenodon Butler, 1946. Late Eocene; Britain.
Dyspterna Hopwood, 1927. Early Oligocene; Britain.
Androconus Quinet, 1965. Early Oligocene; Europe.
Chadronia Cook, 1954. Early Oligocene; North America.
Galethylax Gervais, 1848-52. Late Eocene; Europe.
Buxolestes Jaeger, 1970. Middle Eocene; Europe.

The above generic list follows that of Van Valen (1967) but with the tentative retention of *Opsiclaenodon* and *Bessoecetor* as distinct genera, and the addition of *Buxolestes*.

Simpson (1945) listed *Propalaeosinopa*, *Bessoecetor*, *Palaeosinopa*, and *Pantolestes*. Van Valen (1967) added a new genus *Pantomimus*, *Pagonomus*, *Cryptopithecus*, *Dyspterna*, *Androconus*, *Chadronia* and *Galethylax*. This latter problematical genus (discussion in Van Valen, 1966 : 73; 1967 : 227) was only provisionally referred to the family. Van Valen originally listed a new genus *Pantinomia* from the Middle Palaeocene of North America, as a pantolestid (1967 : 259) but in a later view (1967 : 225, footnote) referred it to the arctocyonids. In the same paper, Van Valen (1967) considered *Bessoecetor* as a synonym (tentative) of *Propalaeosinopa* and *Opsiclaenodon* as a synonym of *Cryptopithecus*, although Russell (*in* Russell, Louis & Poirier, 1966) retained *Bessoecetor* as a valid genus, into which he placed tentatively a new species, *B. levei*. More recently, Dr D. E. Russell (personal communication, 1971) has reaffirmed his belief in the validity of *Bessoecetor*. Russell (1964) in his type description of *Pagonomus* did not assign the genus to a subfamily; he noted resemblances of most of the teeth to the pentacodontine, *Aphronorus*. Additional confirmation of this view was given by a molarised P^4 tentatively referred to the genus by Russell (*in* Russell, Louis & Poirier, 1966). Van Valen (1967) considered the type of *Pagonomus* (an isolated M^2) as a pantolestine.

Genus ***OPSICLAENODON*** Butler, 1946

DIAGNOSIS. Lower molars with moderately elevated cusps, molars uncompressed antero-posteriorly. M_1 and M_2 very similar in size and structure, M_3 much smaller but quite similar structurally. Entoconid moderate-sized and distinct on all molars, hypoconid slightly larger. Hypoconulid of molars small but distinct, not extended posteriorly as a lobe on M_3. Upper molars moderately elongated transversely with rounded outlines; M^1 slightly smaller than M^2, M^3 markedly smaller; prominent hypocone in all molars; conules developed in all molars, situated close to metacone and paracone, the metaconule being larger than the paraconule. In M^2, conules well developed, but more rudimentary in M^1 and M^3. M^1 and M^2 parastylar region extended antero-externally, and metastylar region extended postero-externally, as prominent rounded lobes. No continuous cingulum round base of protocone.

TYPE SPECIES. *Opsiclaenodon major* (Lydekker, 1887). Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. The only known species.

REMARKS. Butler redescribed (1946) *Neurogymnurus major* Lydekker known only from fragmentary lower dentitions, as a new genus *Opsiclaenodon*. In his original description, Butler referred (1946 : 691) *Opsiclaenodon* to the Arctocyonidae, suggesting a relationship with *Dyspterna* and *Didymoconus*. McKenna (*in* Russell and McKenna, 1961 : 281, footnote) suggested that *Opsiclaenodon* was an oxyclaenine arctocyonid, with affinities to *Metachriacus*, *Mimotricentes* and *Spanoxyodon*. Russell (1964 : 193) observed that reference of *Opsiclaenodon* to the Oxyclaeninae was unlikely. Van Valen (1966) referred *Cryptopithecus* and *Dyspterna* to the Pantolestinae. He later added (1967) *Opsiclaenodon* as a synonym of *Cryptopithecus*. Restudy of Butler's material and examination of additional specimens, has confirmed Van Valen's view that *Opsiclaenodon* is a pantolestine. The type of *Cryptopithecus sideroolithicus* is a fragmentary left mandibular ramus with M_2–M_3 (Bayerische Staatssammlung für Paläontologie, Munich, No. A.S. (128) XI 1). Comparison with a cast of this specimen (kindly made available by Dr D. E. Russell) reveals reasonable structural differences (see below) and in the present work, the validity of Butler's genus is accepted provisionally, pending discovery of better more complete material of *Cryptopithecus*.

Isolated M^1 and M^2 (described below) referred to *Opsiclaenodon* show resemblances to the oxyclaenine arctocyonid, *Oxyclaenus*. However, in this genus, the internal margin of the upper molars is more angular and the hypocone is rudimentary; also the lower molars show important differences. The same specimens also show similarity within the arctocyonids to the triisodontine, *Goniacodon*, except for the poor hypocone development in the latter; M_1 and M_2 in these two genera also show similarities. However, these resemblances do not seem significant as *Opsiclaenodon* shows none of the peculiar adaptive features characteristic of the Triisodontinae.

Structurally, the referred upper molars of *Opsiclaenodon* are strikingly similar to some hyopsodontine condylarths such as *Haplaletes* and *Litomylus*. In the latter genus, however, the conules are stronger; tooth outlines are more angular; M^3 is triangular-shaped and lacks a hypocone. Also, P_4 has a metaconid and a small low paraconid. These characteristics (and those of the lower dentition such as P_4 with a metaconid and a small low paraconid) serve to exclude *Opsiclaenodon* from any close relationship with the Hyopsodontidae.

Amongst the described members of the Pantolestinae, *Propalaeosinopa* and *Bessoecetor* are easily distinguished from *Opsiclaenodon* by having slender elevated trigonid cusps; M_3 is much larger and bulbous and P_4 is very elongated with a strong anterior basal cusp and incipient basining of the talonid; M^1–M^2 are very slender and transversely elongated with a smaller hypocone and the outline of M_3 is quite different. In the European species provisionally referred to *Bessoecetor*, *B. levei*, the M^2 and M^3 are more slender and transversely elongated, with angular parastylar and metastylar areas; the lower molars are more angular with more elevated trigonids and the M_3 is longer antero-posteriorly than the other molars, with a posteriorly projecting hypoconulid. The upper molars of *Pantomimus* are more elongated transversely with prominent externally projecting metastylar and parastylar areas; a hypocone is absent. The M^2 (type) of *Pagomomus* is more elongated transversely with more elevated slender cusps and more angular metastylar and parastylar areas; the hypoconal area is more angular and posteriorly extended. In *Pantolestes* the upper molars are similar in shape to *Opsiclaenodon*, but the hypocone is very small and the metastylar and parastylar areas are rounded and less prominent; the lower canine is massive but lacks striations and a groove; the molar paraconid is vestigal and the hypoconulid is strong and posteriorly projecting, in M_3 forming an enlarged posterior lobe. In *Cryptopithecus*, the anterior margin of the molars is more rounded and blunt, with the M_1 paraconid smaller, less elevated and less separated from the protoconid; the trigonid is compressed antero-posteriorly with crowded elevated cusps; the M_1 metaconid is more massive and the talonid cusps are better developed than in *Opsiclaenodon* with a very strong hypoconid. The M_3 in *Palaeosinopa* is as large as M_2; the molar trigonids are slender and more elevated, especially M_3 and the antero-external cingulum is smaller. The upper molars are more elongated transversely with a small hypocone and the posterior mental foramen lies under M_2. *Buxolestes* has a relatively simple canine section; P_4 has a more elongated talonid; M_2 is more rectangular and antero-posteriorly compressed and M_3 is enlarged . In the upper molars of *Buxolestes*, M^2 is more elongated transversely with a less rounded outline and M^3 is triangular-shaped and only slightly reduced with a less developed parastylar area.

Apart from the closely related *Dyspterna* (see later discussion), *Opsiclaenodon* appears nearest structurally to the contemporaneous *Cryptopithecus*. The earlier European history of the family is poorly known and none of the described European species from the Palaeocene and Early-Middle Eocene appear to be closely related to *Opsiclaenodon* and *Cryptopithecus*. The Late Palaeocene and Early Eocene *Palaeosinopa*, however, seems to exhibit the basic dental structure from which *Opsiclaenodon* and *Cryptopithecus* could be derived.

Opsiclaenodon major (Lydekker, 1887)

(Text-figs 16–19)

1887 *Neurogymnurus major* Lydekker: 302
1967 *Cryptopithecus major* (Lydekker); Van Valen: 87

DIAGNOSIS. As for the genus.

LECTOTYPE. B.M. 29718a. Fragment of right mandibular ramus with P_4–M_3 and alveoli of the canine and P_2–P_3. Talonids badly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. Listed Lydekker, 1887 : 302. Figured Butler, 1946, fig. 1; fig. 2, (2), (9).

MATERIAL. All material is from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where otherwise stated.

B.M. 29718. Posterior fragment of left mandibular ramus with M_1–M_3. The coronoid, condyloid and angular processes preserved, though damaged. External surface embedded in matrix. Wear greater than lectotype. Listed Lydekker 1887 : 302. Figured Butler, 1946, fig. 1.

B.M. 36801. Fragment of right mandibular ramus with M_2–M_3. Listed Lydekker, 1887 : 303. Listed Butler, 1946 : 691.

B.M. 36802a. Fragment of right mandibular ramus with alveoli of M_1–M_3. Listed Butler, 1946 : 691.

B.M. 36803. Left mandibular ramus with P_2, M_3 the base of the canine and the alveoli of P_1 and P_3–M_2 Teeth unworn. Listed Lydekker, 1887 : 303. Figured Butler, 1946, fig. 1; fig. 2, (3), (4), (6), (7), (8), (10).

B.M. 36807. A crushed fragment of left mandibular ramus with M_2–M_3 and alveoli of P_4–M_1. External surface embedded in brown clayey sand matrix. Teeth unworn. Listed Lydekker, 1887 : 303. Figured Butler, 1946, fig. 2, (1), (5).

S.M. C53478. Isolated right M_1. Unworn. Damaged metaconid.

B.M. M12565b. Isolated right M_1. Unworn.

S.M. C30611. Fragment of left mandibular ramus with P_3–P_4 and alveoli of M_1, bases of alveoli of P_2 and the canine. Unworn.

S.M. C54162. Isolated teeth. All from Lower Headon Beds (Rodent Bed), Hordle Cliff.

a. Right P_2. Unworn.
b. Right M_2. Part worn.
c. Right M_2. Part worn.
d. Right M_2. Part worn.
e. Left M_1. Part worn.

B.M. 29863. Anterior fragment of left mandibular ramus with the canine, P_2–P_4, and alveolus of P_1. Tip of canine broken off. Symphysis preserved. Matrix of brown clayey sand.

B.M. M25094. Anterior fragment of right mandibular ramus with P_3 and alveoli of the canine, P_1, P_2, P_4 and M_1. Posterior part of symphysis preserved.

B.M. 25084. Isolated right lower canine. Tip damaged.

B.M. M25091. Isolated right M_3. Moderately worn.

S.M. C30713. Isolated right upper molar (M^2?). Unworn.

S.M. C30722. Isolated left upper molar (M^2?). Badly worn.

S.M. C9677. Isolated left upper molar (M^3?). Unworn.

S.M. C54163. Isolated right upper molar (M^1?). Moderately worn.

Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The mandible is moderately elongated and stout with a slight anterior deepening. The symphysial surface (B.M. M25094, B.M. 36803 and B.M. 29863) is elongated and oval in outline, ending posteriorly below P_2. The posterior region of the mandible is preserved only in B.M. 29718: the condyle, situated above the level of the tooth row is damaged, but appears to have been transversely elongated. The angular and coronoid processes are separated from the condyle by fairly prominent notches. The masseteric fossa extends only slightly below the level of the tooth row; the mandibular foramen is situated similarly. The anterior mental foramen occurs below P_1/canine (B.M. 36803 and B.M. 29718a) or below P_1 (B.M. M25094 and B.M. 29863). The posterior mental foramen is also variably sited below P_4 (B.M. 36803 and B.M. 29718a) or M_1 (B.M. 36802a, B.M. 25094 and S.M. C30611). An additional small foramen occurs below P_3 (B.M. 29863 and B.M. 36803) or below P_2 (B.M. M25094).

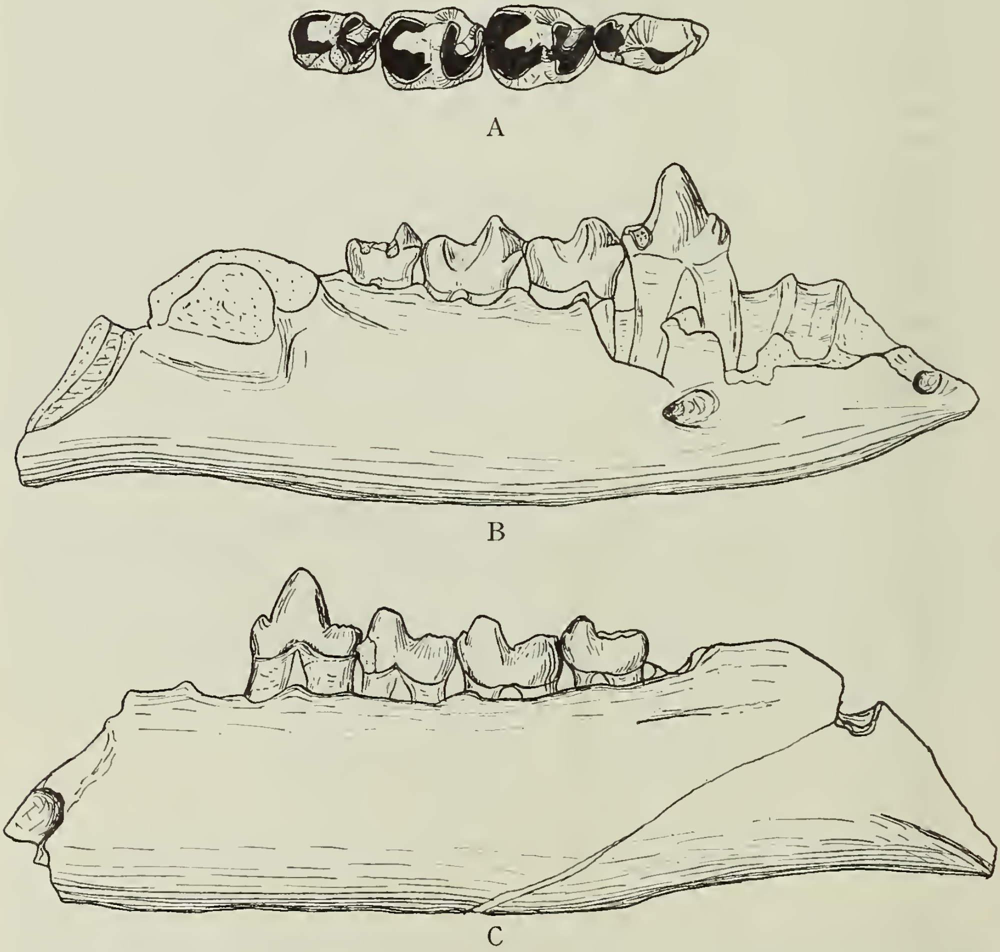

Fig. 16. *Opsiclaenodon major* (Lydekker, 1887). Fragmentary right mandibular ramus with P_4–M_3. Lectotype (B.M. 29718a) approx. ×3·5. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

The lower incisors are not known. The lower canine is known from B.M. 36803, B.M. 29863 and B.M. M25084. The upper half of the tooth is enamel covered; this enamel is wrinkled externally, forming regular striations. The upper half of the tooth is triangular in section with sharp postero-external, internal and antero-internal crests; the latter two crests bound a prominent groove. In B.M. 36803 and B.M. 29863 the groove, crests and enamel covering occur below alveolar level, but in these specimens, the tooth is incompletely erupted. These features are considered to occupy the upper half of the tooth, by analogy with material of *Dyspterna* (described later) where an almost identical tooth is fully developed and completely preserved. Butler, in his type description (1946 : 694) observed that the canine of B.M. 36803 was grooved and incompletely erupted, but did not record the curious external striations of the enamel and the enamel distribution. In B.M. 29718a the canine alveolus extends to the posterior end of the symphysis; in S.M. C30611 and B.M. M25094, it extends posterior to this.

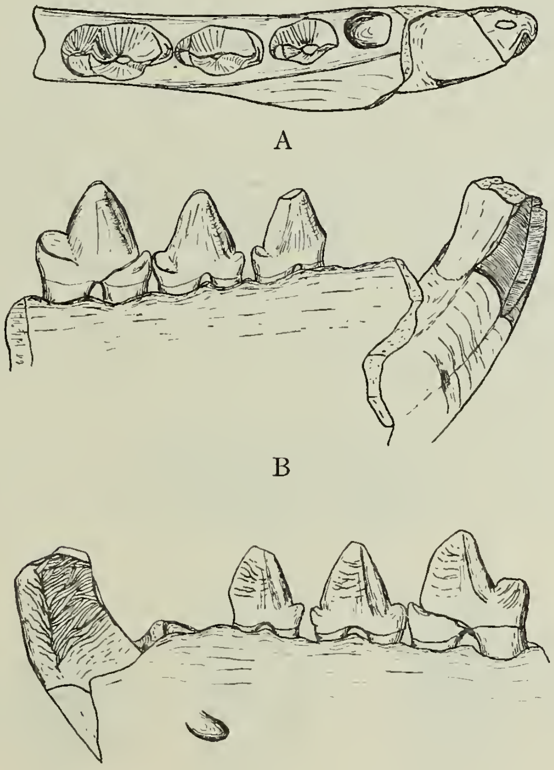

Fig. 17. *Opsiclaenodon major* (Lydekker, 1887). Fragmentary left mandibular ramus with C, P_2–P_4. B.M. 29863 ×3·5. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

P_1 from its alveolus (B.M. 36803, B.M. 29863 and B.M. M25094) was evidently small, single-rooted and placed immediately posterior to the canine. P_2 is preserved in B.M. 36803, S.M. C54162a and B.M. 29863; the tooth is double-rooted and has a slight forward inclination. From a single large anterior cusp, steep posterior and postero-internal crests fall to the antero-external and antero-internal extremities, respectively of a small slightly basined heel. An anterior crest from the main cusp curves internally at the anterior tooth margin forming a faint cingulum. On the antero-internal wall of the tooth, just posterior to the anterior crest, there is a vertical groove, similar to though less pronounced than that of the canine. Horizontal striations similar to those of the canine, are well developed externally on the main cusp in B.M. 29863 and S.M. C54162a, though less prominent on B.M. 36803. P_3 is known from S.M. C30611 and B.M. 29863; these specimens were not listed by Butler (1946) who described only alveoli of this tooth. The tooth is generally similar to P_2 but larger with a large crested main cusp. The anterior crest curves internally at the base of the antero-internal groove forming a very faint cingulum-like cuspule (S.M. C30611) or a strong low cusp (B.M. 29863). The posterior crest continues antero-posteriorly across the middle of the well developed heel. Externally, there is some development of irregular, subhorizontal enamel striations. P_4 (B.M. 29718a, S.M. C30611 and B.M. 29863) is very similar in structure to P_3 but much larger. The antero-internal groove is marked clearly on S.M. C30611 and B.M. 29863, but less prominent on B.M. 29718a. According to Butler (1946 : 695), the groove is absent in B.M. 29718a, the only specimen containing P_4 listed by him. The antero-posterior talonid crest in S.M. C30611 swells posteriorly to form a cusp; in B.M. 29863, the median region of the crest is raised as a distinct cusp. Two small internal cuspules occur on the talonid of B.M. 29718a; these are absent in the other specimens.

M_1–M_3 are structurally very similar with rounded trigonid and talonid margins; M_1 and M_2 are subequal; M_3 is markedly smaller. Identification of isolated teeth

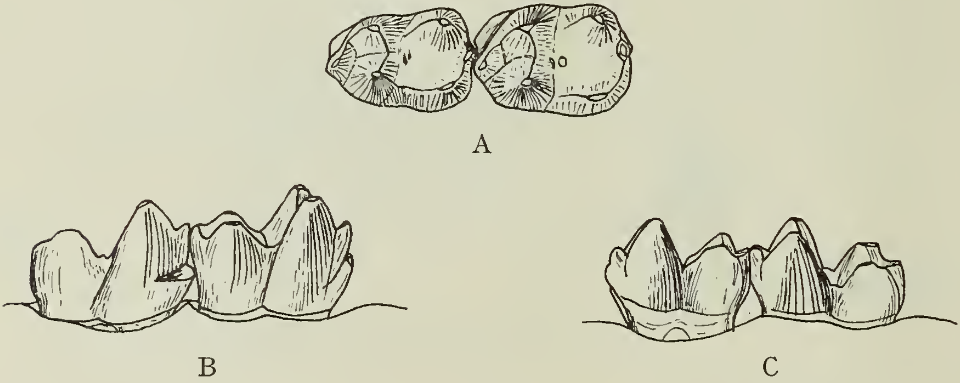

FIG. 18. *Opsiclaenodon major* (Lydekker, 1887). Composite right M_1–M_2 all approx. ×5. M_1 (B.M. M12565b) and M_2 (S.M.C 54162d). Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

as M_1 or M_2 is uncertain; M_1 has been distinguished here by a slight anterior narrowing of the trigonid. The metaconid and protoconid are subequal (when unworn), opposite and transversely crested. The small though distinct low paraconid is median or slightly internal to the midline, forming the fairly sharp anterior apex of the tooth; a crest from this cusp meets the anterior protoconid crest. A fairly strong shelf-like antero-external cingulum is present. The hypoconid and entoconid are prominent and opposite, the hypoconid being slightly larger; each cusp is united to the posterior trigonid wall by sharp crests. The hypoconulid is small, though distinct; it is strongly posterior to the hypoconid and entoconid, and posteriorly projecting; the cusp is usually slightly external to the midline and is joined to the hypoconid and entoconid by low crests. This condition is seen in the M_3 of B.M. 36807, but this cusp in the M_3 of B.M. 29718 and B.M. 36803 is distinct and median. The talonid is strongly basined. Small accessory crests and cuspules are variably developed in the molars: in B.M. 36803, B.M. 36807 and B.M. M25091, a discontinuous crest swings obliquely down the posterior trigonid wall from the metaconid towards the crista obliqua; this cannot be distinguished in other specimens owing to excessive wear. On M_2 of B.M. 36807 and S.M. C54162d, there is a small cuspule in the middle of the talonid at the base of the posterior trigonid wall. This is absent in S.M. C54162b and S.M. C54162c. In other specimens wear is too great for this feature to be distinguished.

The upper teeth are known only in the isolated state. S.M. C30713 and S.M. C30722, almost identical structurally, are the largest teeth; these are considered as M^2. S.M. C54163 is somewhat smaller antero-posteriorly, showing several minor structural differences; this is tentatively considered as M^1. S.M. C9677, markedly smaller in length and width than the other teeth, probably represents M^3. M^2 is elongated transversely and has a rounded outline. The antero-internal crescentic protocone, the largest cusp, dominates the internal half of the tooth. The conical paracone is subequal in height with the protocone; the metacone is smaller. There is a strong shelf-like external and postero-external cingulum round the metacone base, ending externally as a small mesostyle, and a similar anterior cingulum round the base of the paracone (not present externally). The parastylar region is extended antero-externally, the metastylar region extended postero-externally, as rounded lobes. The sharp postero-externally trending protocone crest is interrupted just internal to

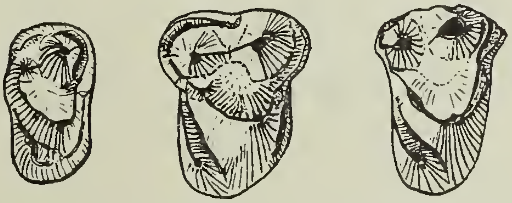

FIG. 19. *Opsiclaenodon major* (Lydekker, 1887). Occlusal view of composite M^1–M^3 ×5. Right M^1 (S.M. C54163), right M^2 (S.M. C30713) and left M^3 (S.M. C9677), drawing reversed. Lower Headon Beds, Hordle Cliff.

the metacone by a prominent metaconule. A smaller paraconule is similarly placed on the protocone crest just internal to the paracone. There is a small low anterior cingulum and a very strong shelf-like postero-internal cingulum which supports externally a very strong hypocone which is subequal in height with the metacone. S.M. C30722, a well worn M^2, has a more developed anterior cingulum. M^1 is basically similar to M^2 and although the tooth is more worn than M^2 (S.M C30713) and damaged externally, significant differences can still be recorded: the tooth is shorter antero-posteriorly than M^2. The hypocone and hypocone-cingulum are less developed; the metaconule is very small and the paraconule, just distinguishable on the slightly worn crest must have been very rudimentary on the unworn tooth. The postero-external cingulum round the base of the metacone is absent and there is only a trace of the antero-internal cingulum. M^3 is basically similar to the other molars but much smaller and compressed antero-posteriorly. The metaconule is very small, merging with the antero-external cingulum and an internal paracone crest. The antero-external trending protocone crest joins the paracone; a small swelling on this crest just internal to the paracone indicates a rudimentary paraconule. A small postero-external cingulum is present, but not round the metacone base as in M^1 and M^2; this latter cusp, slightly smaller than the hypocone, is more antero-internal than in M^1 and M^2.

REMARKS. There is considerable variation in the depth of the mandible: B.M. 29718a is greatest, B.M. 29718 intermediate, and B.M. 36803 smallest in size. B.M. 36803 has unworn teeth and an incompletely erupted canine, indicating derivation from a very young individual. This suggests that the variation in mandible depth is, at least in part, related to individual age differences. There are slight variations in the positions of the mental foramina; in the degree of prominence of the antero-

TABLE 10

Measurements (in mm) of *Opsiclaenodon major*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 29718	—	—	—	—	—	—	4·1	3·3	4·2	3·3	3·7	2·8
B.M. 29718a	—	—	—	—	4·5	2·3	4·0	3·4	4·1	3·3	3·4	2·6
B.M. 36807	—	—	—	—	—	—	—	—	4·4	3·3	3·5	2·6
B.M. 36802	—	—	—	—	—	—	—	—	4·3	2·9	3·2	2·3
B.M. M12565b	—	—	—	—	—	—	4·2	3·2	—	—	—	—
B.M. 36803	3·1	1·8	—	—	—	—	—	—	—	—	3·5	2·6
B.M. 29863	3·0	1·8	3·6	2·0	4·5	2·4	—	—	—	—	—	—
B.M. M25094	—	—	3·6	2·0	—	—	—	—	—	—	—	—
B.M. M25091	—	—	—	—	—	—	—	—	—	—	3·2	2·6
S.M. C53478	—	—	—	—	—	—	3·8	3·0	—	—	—	—
S.M. C54162a	3·0	1·7	—	—	—	—	—	—	—	—	—	—
,, ,, b	—	—	—	—	—	—	—	—	4·4	3·2	—	—
,, ,, c	—	—	—	—	—	—	—	—	4·1	3·2	—	—
,, ,, d	—	—	—	—	—	—	—	—	4·4	3·4	—	—
,, ,, e	—	—	—	—	—	—	4·3	3·2	—	—	—	—
S.M. C30611	—	—	3·7	1·9	4·2	2·4	—	—	—	—	—	—

internal groove and antero-external enamel striations in the premolars, and in the development of accessory cuspules. These have been considered in the preceding description.

Genus *DYSPTERNA* Hopwood, 1927

Diagnosis. Lower molars with low blunt cusps, M_3 trigonid rather compressed antero-posteriorly. M_1 and M_3 probably subequal in size, M_2 larger. Entoconid of molars vestigial or absent with postero-internal talonid margin raised as a crest, hypoconid large. Hypoconulid of molars median and small to vestigial.

Type species. *Dyspterna woodi* Hopwood, 1927. Early Oligocene ('Sannoisian'), Yarmouth, Isle of Wight.

Remarks. The genus was originally based by Hopwood on a single specimen, from the Lower Hamstead Beds, a very fragmentary worn and damaged mandibular ramus with M_2–M_3 (B.M. M13125), provisionally placed in the Oxyclaeninae. Three years later, Dal Piaz described (1930) a maxillary fragment with P^4–M^3 which he tentatively referred to Hopwood's species. This specimen was removed by Van Valen (1966 : 88) from *Opsiclaenodon* as the type of a new apheliscine, *Epapheliscus italicus* Van Valen, 1966. Dal Piaz also described a new species (1930 : 13) which he tentatively referred to the genus as ?*Dyspterna helbingi*; the holotype (and only known specimen) is a fragmentary left maxilla with P^3 and the roots of P^4–M^3. Recently, Van Valen has observed (1966 : 88) that from the published figure and description, the affinities of this specimen cannot be determined.

In his redescription of *Neurogymnurus major* as *Opsiclaenodon major*, Butler suggested (1946 : 698) a possible relationship with *Dyspterna woodi*. The genus was not listed by Simpson (1945) being based on inadequate material, and McKenna stated (*in* Russell & McKenna, 1961 : 281, footnote 3) that *Dyspterna* constitutes practically a *nomen dubium*. Van Valen (1966 and 1967) referred *Dyspterna* to the Pantolestidae.

In the present work, material collected fairly recently from the Upper Headon Beds has been referred to *Dyspterna* (on the basis of molar structure) as a new species. The anterior lower dentition of this species of *Dyspterna* is strikingly similar to that of *Opsiclaenodon* and the two genera appear to be closely related, thus supporting Butler's original view.

Opsiclaenodon is distinguished generically from *Dyspterna* by the uncompressed M_3 trigonid; the molar entoconid is strongly developed; the hypoconulid is well defined and the cusps are more trenchant and separated. The prominent hypoconid and vestigial or absent entoconid sharply distinguishes *Dyspterna* from all other pantolestines. These and other specialised features could have arisen by modification of a dental structure similar to that of *Opsiclaenodon*.

Van Valen has stated (1967 : 227) that *Opsiclaenodon* could be directly ancestral to *Dyspterna*. This possibility is precluded by the contemporaneous occurrence of *Dyspterna hopwoodi* sp. nov. and *Opsiclaenodon major* in the Headon Beds; both genera were probably derived from an earlier common ancestry, perhaps in the Middle Eocene.

Dyspterna hopwoodi sp. nov.

(Text-figs 20, 21)

ETYMOLOGY. After A. T. Hopwood.

DIAGNOSIS. M_1 and M_3 hypoconid large, entoconid and hypoconulid vestigial, appearing as small swellings on postero-internal marginal crest. Crista obliqua in M_1 and M_3 directed anteriorly to base of prococonid. M_3 trigonid more compressed antero-posteriorly than in *D. woodi*, with the small paraconid strongly antero-internal in position, close to metaconid; M_3 hypoconulid vestigial. Sharp condyloid and coronoid crests bordering deep masseteric fossa.

HOLOTYPE. B.M. M26052. Right mandibular ramus with the canine, P_2–P_4 and M_3, and alveoli of I_1–I_3, P_1 and M_1–M_2. Symphysis and posterior region of mandible are preserved. Slightly worn dentition. Upper Headon Beds (Lignite Bed), Headon Hill.

PARATYPES. B.M. M26053. Isolated right M_1. Slightly worn. Upper Headon Beds (Lignite Bed), Headon Hill.

B.M. M26054. Isolated right P_1. Unworn. Upper Headon Beds (Lignite Bed), Headon Hill.

DESCRIPTION. The mandible is moderately stout with a slight anterior deepening as in *Opsiclaenodon*. The symphysis is elongated and rectangular in outline, ending posteriorly under P_2 and inclined at about 45° to the level of the tooth row. The posterior region of the mandible is complete in the holotype, except for the condyle which lay just above the level of the tooth row. The coronoid process is well developed and massive, the anterior edge rising steeply from the tooth row level. The notch between the condyle and the coronoid is hardly perceptible; this is in contrast to *Opsiclaenodon*, where it appears to have been more developed. The angular is fairly prominent and well separated from the condyle; the lower edge is deflected internally as a small flange. The mandibular foramen is situated just below alveolar level; the ridge above this running from the condyle to a position below M_3 is more prominent than in *Opsiclaenodon*. The anterior mental foramen is sited below the canine/P_1, the posterior mental foramen below M_1.

The bases of the alveoli of I_1–I_3 indicate that these teeth were closely crowded and situated immediately anterior to the canine. The canine is almost identical to that of *Opsiclaenodon major* with the upper half of the tooth enamel covered; externally the enamel is wrinkled, forming regular striations. The upper half of the tooth is triangular-shaped with sharp antero-internal, internal and postero-external crests, and a prominent deep antero-internal groove. The groove and crests are confined mainly to the enamel-covered upper half of the tooth. Below this level, the crests become rounded but the groove, in contrast to *Opsiclaenodon major* is continued to alveolar level as a distinct but rounded constriction. From the alveolus in the holotype, it appears that P_1 was a little separated from the canine; the tooth (B.M. M26054) is single-rooted with a main central cusp and a small postero-internal heel. The cusp is crested anteriorly, postero-internally and posteriorly. There are small but distinct antero-internal and postero-external cingula and a cingulum trace antero-externally. A rudimentary antero-internal groove is present.

P_2 is slightly larger than P_1 and double-rooted. There are no antero-external and postero-external cingula; otherwise the tooth is structurally nearly identical to P_1. There is the suggestion of a slight antero-internal groove. P_3 is identical to P_2, except for a larger size and a slightly stronger cusp-like antero-internal cingulum. There is a trace of an antero-internal groove. P_4 is structurally quite similar to P_3 but much larger. The sharp anteriorly crested main cusp falls to a prominent low anterior cusp; this latter cusp is larger than that of *Opsiclaenodon* and the tooth is generally more pointed. There are small antero-external and antero-internal cingula. The antero-posterior talonid crest ends posteriorly in a small cusp. There is a slight antero-internal groove.

It is difficult to estimate reliably the relative sizes of M_1 and M_2 from the alveoli in the holotype of *D. hopwoodi* because of mandible damage. By comparison with the holotype of *D. woodi* (about the same size as *D. hopwoodi*) where M_3 is smaller than

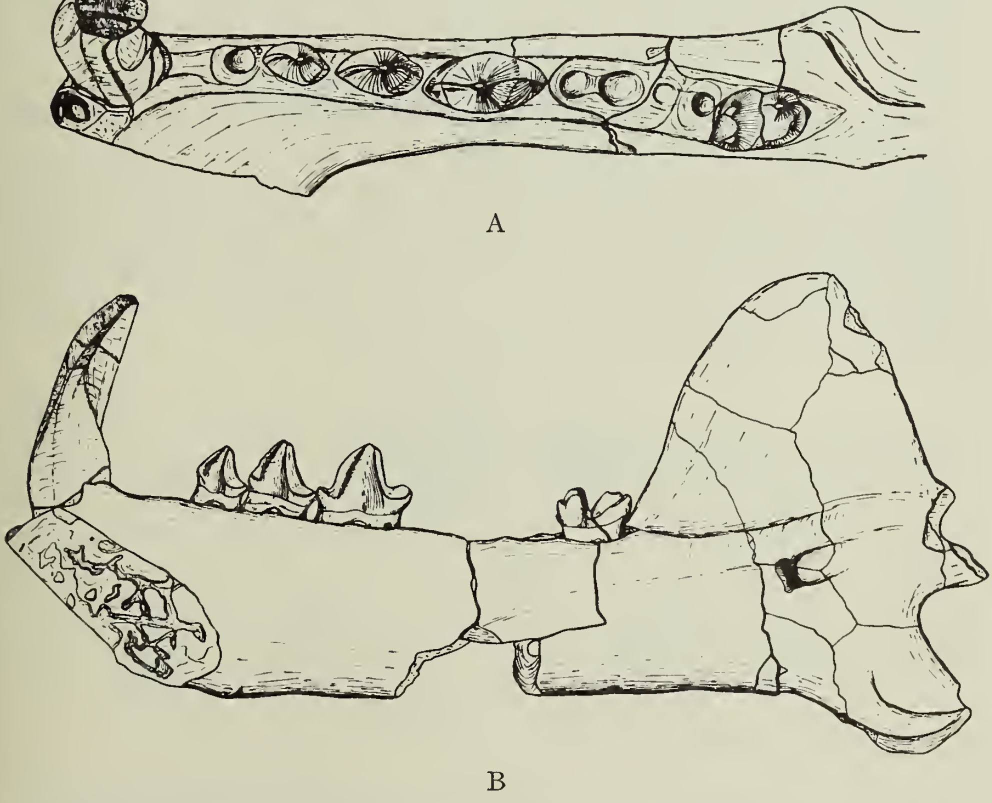

Fig. 20. *Dyspterna hopwoodi* sp. nov. Right mandibular ramus with C, P_2–P_4 and M_3. Holotype (B.M. M26052). Upper Headon Beds, Headon Hill. (A) Occlusal view ×2·5. (B) Internal view ×2.

M_2, it has been concluded that an isolated molar (paratype) of *D. hopwoodi* is best considered as M_1. This latter tooth is elongated with a rounded margin. The protoconid and metaconid are subequal, opposite and transversely crested. The small but distinct low median paraconid forms the sharp anterior apex of the tooth. There is a moderately strong antero-external cingulum and a smaller antero-internal cingulum. The entoconid and hypoconid are vestigial, appearing as small swellings on a low curved crest which forms the postero-internal talonid margin. The median hypoconulid projects slightly posteriorly; the entoconid and hypoconid are opposite each other. The talonid is slightly basined. M_3 is almost the same length as M_1, with a subequal and opposite protoconid and metaconid. The smaller paraconid is strongly internal and anterior to the metaconid; the trigonid appears antero-posteriorly compressed. The almost straight antero-external trigonid margin is formed by a paraconid and protoconid crest. There is a small antero-external cingulum but the antero-internal cingulum is absent. The vestigial hypoconulid is represented by a minute rounded median lobe which is posteriorly projecting and separated from the larger hypoconid. The entoconid is vestigial; a low rounded crest runs anteriorly from the hypoconulid-lobe, forming the postero-internal tooth margin. The talonid is only very slightly basined.

REMARKS. In the canine of the holotype (B.M. M26052) distinct wear facets are visible: part of the postero-external face has been gauged away by the upper canine in occlusion, to form above alveolar level, a prominent oblique baso-exteriorly directed shelf. Wear has taken place along the whole vertical length of the tooth from the tip to this shelf, but becomes progressively greater towards this latter position; presumably slight wear took place near the canine tip when the tooth was partially erupted (compare *Opsiclaenodon major*, B.M. 29863). Anteriorly and basally to the prominent groove, there is a shallow vertical oval facet, produced probably by friction against one of the upper incisors.

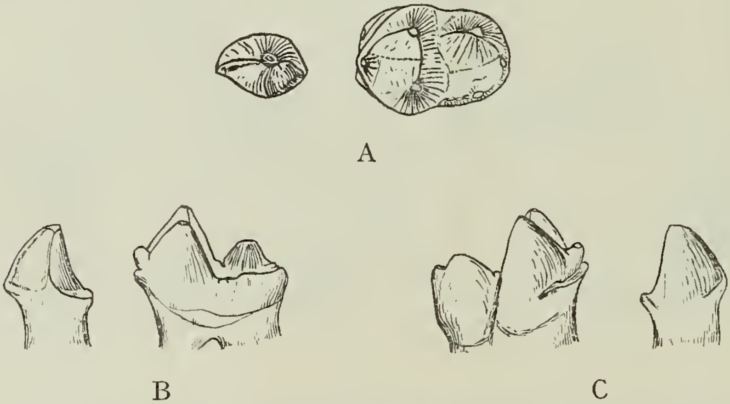

FIG. 21. *Dyspterna hopwoodi* sp. nov. Right P_1 (B.M. M26054) and right M_2 (B.M. M26053). Both ×4. Upper Headon Beds, Headon Hill. (A) Occlusal view. (B) Internal view. (C) External view.

The antero-internal groove does not show any signs of wear; the bordering crests are very sharp and quite unworn. The same situation exists in the closely similar canine of *Opsiclaenodon major.* As Butler noted (1946 : 695), a similar unworn groove occurs on the lower canine of *Nasua,* a recent procyonid. No information has been found about the significance of this groove in *Nasua.* On the available evidence, the structure in all three genera would appear to be non-functional, at least in occlusion.

In molar structure, *D. hopwoodi* is closely related to the type species, *D. woodi* and may be ancestral to the latter. *D. hopwoodi* sp. nov. appears specifically distinct on the basis of the following differences: in *D. woodi,* the hypoconid crest is directed antero-internally to meet the base of the metaconid, in M_3 running up the posterior wall of the metaconid; the cingula are relatively larger and more shelf-like; the M_3 trigonid is less compressed antero-posteriorly with the paraconid slightly more median; the hypoconulid appears to have been relatively larger, and the coronoid and condyloid processes are lower and more rounded, enclosing a shallower masseteric fossa. More detailed comparison is not possible because of the poor preservation of the holotype of *D. woodi.*

TABLE II

Measurements (in mm) of *Dyspterna hopwoodi*

	P_1		P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. M26052	—	—	3·6	2·3	4·7	2·8	6·6	3·3	—	—	—	—	5·0	3·6
B.M. M26053	—	—	—	—	—	—	—	—	5·4	3·7	—	—	—	—
B.M. M26054	3·4	2·9	—	—	—	—	—	—	—	—	—	—	—	—

Family **APATEMYIDAE** Matthew, 1909

DIAGNOSIS. Genera with a reduced dental formula—probably $\frac{2}{1}, \frac{0}{0}, \frac{2}{2}, \frac{3}{3}$. Jaw deep and stout in proportion to molars, with posterior mental foramen below M_1 or M_2. Marked soricid-like development of lower incisors, the roots of which terminate below M_3. P_3 blade-like and single-rooted. Molars in early forms trenchant; more typically, bunodont and primate-like in appearance. P^3–P^4 double-rooted and unicuspid. Upper molars relatively elongated antero-posteriorly and broadly expanded postero-internally with a well developed hypocone, but lacking a mesostyle. Lower molars, except for M_3, have a simple talonid but the trigonid, particularly in M_2–M_3 shows a distinctive parallelogram arrangement of cusps and crests. (Mainly after Gazin, 1958).

REMARKS. Of the seven genera assigned to the family, five are known from North America and two from Europe:

Jepsenella Simpson, 1940. Middle Palaeocene; North America.
Labidolemur Matthew & Granger, 1921. Late Palaeocene; North America.
Apatemys Marsh, 1872. Early-Late Eocene; North America.

Stehlinella Matthew, 1929. Late Eocene; North America.
Sinclairella Jepsen, 1934. Early-Middle Oligocene; North America.
Eochiromys Teilhard de Chardin, 1927. Early Eocene; Belgium.
Heterohyus Gervais, 1848-52. Middle-Early Eocene; Europe.

Van Valen (1967) considered *Teilhardella* Jepsen, 1930 was invalid and included it within *Apatemys*. In addition to the above generic list, McKenna (1963 : 30) suggested that *Unuchinia* Simpson, 1937, previously placed *incertae sedis* in the Insectivora, might be an apatemyid. More recently, Van Valen (1967) formerly erected a new subfamily Unuchiniinae Van Valen & McKenna, for the reception of *Unuchinia*.

Stehlinella is known from the anterior portion of the skull with part of the upper dentition and an almost complete mandibular ramus lacking only P_4. *Sinclairella* is known from a complete but crushed skull with part of the upper dentition and a mandibular ramus lacking P_3–P_4 and M_1. The remaining six genera are based on fragmentary mandibles, although *Heterohyus* is known also from a palatal fragment.

Owing to incomplete material and the comparative rarity of specimens, classification is very tentative. Some genera are probably composite but better material is needed before significant advances can be made.

The family has oscillated between Primates and Insectivora for many years. The most recent detailed work on the affinities of this problematical group is McKenna (1963). From a consideration of molar structure in the earliest genera, McKenna referred the family to the Insectivora; this view, followed by Van Valen (1967) is adopted here.

Genus ***HETEROHYUS*** Gervais, 1848–52

Diagnosis. Usually single mental foramen below M_2; fossa below P_4 generally reduced. Enamel covering lower incisors extends into alveolus but does not completely coat the crown; P_4 generally reduced; M_3 talonid usually strongly elongated and M_3 posterior trigonid wall usually oblique to longitudinal axis of tooth.

Type species. *Heterohyus armatus* Gervais, 1848-52. Middle Eocene (Early Lutetian); Bouxwiller, France.

Remarks. Distinguished from the other genera as follows: *Jepsenella* shows only incipient development of apatemyid characteristics; in *Eochiromys* and *Labidolemur* the incisor crown is completely covered by enamel. These genera and all other apatemyids possess either a little-elongated M_3 talonid or lower molars with a transverse posterior trigonid wall.

Five species have been distinguished:

H. armatus Gervais, 1848-52, pl. 35, fig. 14. Middle Eocene (Early Lutetian); France.

H. quercyi (Filhol, 1880), p. 174, figs 1–3. Late Eocene (Early Ludian, Quercy Phosphorites); France.

H. nanus Teilhard de Chardin, 1922, p. 93, fig. 41; pl. 4, fig. 21. Late Eocene (Early Ludian, Quercy Phosphorites); France.

H. europaeus (Rütimeyer, 1890), p. 346, figs 1–2. Middle Eocene (Early-Middle Lutetian); Switzerland.

H.heufelderi Heller, 1930, p. 32, pl. 5, fig. 4. Middle Eocene (Lutetian); Germany.

The most complete species, *H. quercyi*, is based on a crushed skull and almost complete upper dentition and a fragmentary mandibular ramus; *H. nanus* and *H. armatus* are based on mandibular fragments, *H. heufelderi* on a complete lower dentition. The type of *H. armatus* (the type species) was not located by Teilhard de Chardin (1922 : 89) and here, is considered to be lost.

Stehlin (1916 : 1462) erected the genus *Heterochiromys* for two species from Egerkingen: *H. gracilis* known from mandibular rami lacking teeth and isolated incisors, and *H. fortis* based on isolated incisors. It is highly probable, as suggested by Teilhard de Chardin (1922 : 92), that *Heterochiromys gracilis* Stehlin is synonymous with *Heterohyus quercyi* (Filhol) and *Heterochiromys fortis* Stehlin, is synonymous with *Heterohyus armatus* Gervais. Stehlin (1916 : 1434) also placed several mandibular rami lacking teeth, and isolated incisors from Egerkingen in a new genus and species, *Amphichiromys europaeus*. This was based on minor differences in the incisors. Isolated lower molars tentatively assigned by Stehlin to this genus are of characteristic heterohyid type and apparently do not warrant generic separation. The genus is considered synonymous with *Heterohyus*.

The generic diagnosis is unsatisfactory and probably, *Heterohyus* is a composite genus. *H. nanus* does not fit well into this diagnosis and appears to be indistinguishable from *Apatemys bellus*. American material has not been examined, so this view is only tentative.

The material described below, constitutes the first record of an apatemyid from the Tertiary of Britain.

Heterohyus sp.

(Text-fig. 22)

MATERIAL. S.M. C54172. Isolated left M3. Moderately worn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. This strongly elongated tooth is composed mainly of a gently basined talonid, the latter being $2\frac{1}{2}\times$ the length of the trigonid. The trigonid is wider than the talonid and externally projecting. The low blunt cusps and crests of the trigonid exhibit a distinctive parallelogram arrangement.

The metaconid and paraconid are almost equal in size, the antero-internal paraconid being directly anterior to the metaconid; these cusps are united by a massive antero-posterior crest. The smaller protoconid is moderately separated from the metaconid and paraconid, and more anteriorly placed in relation to the metaconid; the posterior trigonid wall is thus markedly oblique to the longitudinal axis of the tooth. From the paraconid a small low crest runs parallel to the posterior trigonid wall, forming the oblique anterior tooth margin. The antero-external extremity of the tooth, directly anterior to the protoconid, is sharp and acute-angled; here, the crest is very faint and low.

The talonid basin is bounded externally and internally by rounded fairly strong crests which are almost parallel. The higher crista obliqua meets the posterior trigonid wall midway between the metaconid and protoconid; the internal crest is continued faintly up the posterior wall of the metaconid. The internal talonid margin is damaged; it may have curved out internally, with a more rounded outline than the external margin. Around the posterior edge of this damaged area is the possible trace of a small entoconid. From this position, the straight talonid margin runs to a relatively high rounded externally shifted hypoconulid-lobe. From the entoconid, a minute crest dilates as it curves round to meet a prominent hypoconulid, in the anterior part of the hypoconulid-lobe. No hypoconid is distinguishable, although the tooth is damaged anterior to the hypoconulid; a small cusp may have been present.

The total antero-posterior length of M3 is 5·8 mm; the trigonid length is 1·6 mm, that of the talonid 3·7 mm. The trigonid transverse width is 2·9 mm, the talonid width is 2·2 mm.

REMARKS. This specimen is distinguished from the M3 of known species as follows: *H. nanus* is much smaller with a short talonid and a slightly oblique trigonid; *H. quercyi* is much smaller with a slightly oblique trigonid; *H. europaeus* is larger with a slightly oblique trigonid; *H. heufelderi* is smaller with a relatively shorter talonid and in *H. armatus* the talonid is less elongated and wider transversely than the trigonid. Also, the tooth outline in all the above is more prominently rounded.

The Headon Beds specimen appears closest to *H. armatus*. However, little is known about variation within the genus; the known species are restricted to the

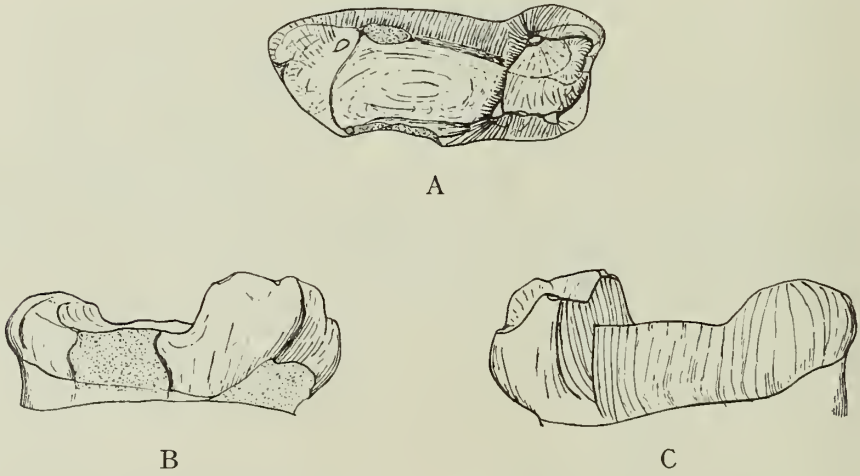

FIG. 22. *Heterohyus* sp. Left M3. S.M. C54172 approx. ×8. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) Internal view. (C) External view.

Lutetian and Early Ludian and the genus already may be oversplit. S.M. C54172 could represent a distinct new species but better material is needed. At present the specimen seems best recorded as *Heterohyus* sp.

TABLE 12

Measurements (in mm) of M3 of *Heterohyus* species

	Total a-p length	Ratio of trigonid length to talonid length	Angle between posterior wall of trigonid and longitudinal axis
H. heufelderi (*ex* Heller, 1930)	4·0	—	—
H. quercyi (*ex* Teilhard de Chardin, 1922)	3·9	1 : 2½	100°
H. nanus (*ex* Teilhard de Chardin, 1922)	2·5	1 : 1½	105°
H. armatus (*ex* Gervais, 1848-52)	7·0	1 : 2	130°
H. europaeus (*ex* Stehlin, 1916)	9·0	1 : 2½	100°
H. sp. (S.M. C54172)	5·8	1 : 2½	120°

Order PRIMATES

Family **ADAPIDAE** Trouessart, 1879

DIAGNOSIS. Dental series usually continuous—no marked diastema. Incisors typically wide-crowned and trenchant; upper canines straight, lower canines short, subpremolariform. Upper molars tritubercular or quadritubercular with a large V-shaped protocone; small but true hypocone derived from posterior cingulum; mesostyle usually absent. Paraconid absent or much reduced on lower molars; entoconid retarded; hypoconulid absent or rudimentary except on M3. Mandible generally short and stout with a greatly expanded angular and a high recurved coronoid process. Condyle elongated transversely and relatively flattened. Skull usually with high sagittal and lambdoidal crests. Small ovoid braincase. Prominent heavy facial region. (after Hill, 1953).

REMARKS. Simons (1962) presented a revised classification of European Eocene primates. This revision, together with Gazin's revival (Gazin, 1958 : 31) of the family Notharctidae Trouessart, 1879, has significantly altered Simpson's classification of 1945. The generic list follows Simons (1962) with the addition of *Lantianus* Chow, 1964.

Adapis Cuvier, 1822. Middle-Late Eocene; France, Britain, Switzerland.
Pronycticebus Grandidier, 1904. Late Eocene; France.
Anchomomys Stehlin, 1916. Middle-Late Eocene; France, Switzerland.
Caenopithecus Rütimeyer, 1862. Middle Eocene; Switzerland.
Protoadapis Lemoine, 1878. Early-Late Eocene; France, Germany.
Gesneropithex Hürzeler, 1946. Late Eocene; Switzerland.
Lantianus Chow, 1964. ?Late Eocene; China.

In addition to *Caenopithecus*, Simpson, (1945) considered two further genera as Adapidae *incertae sedis*: *Aphanolemur* Granger & Gregory, 1917 and *Amphilemur* Heller, 1935. *Aphanolemur* is now believed to be a synonym of *Smilodectes* Wortman, 1903, a notharctid (Gazin, 1958 : 30). *Amphilemur* has been considered by McKenna (1960 : 58) as an erinaceoid insectivore. More recently, Simon's generic list has been accepted by McKenna (1967) and Russell, Louis & Savage (1967) although the latter authors regarded reference of *Gesneropithex* as provisional and tentatively added *Periconodon* Stehlin, placed by Simons (1962) and McKenna (1967) in the Omomyidae.

Genus *ADAPIS* Cuvier, 1822

SYNONOMY. See Hill, 1953 : 464.

DIAGNOSIS. Mandible has a greatly expanded angular process; coronoid process separated from condyle by a fairly shallow notch. P_1 present, small in size; P_4 submolariform but cusps variably developed; M_1 and M_2 similar to P_4; M_3 considerably elongated by hypoconulid which is not isolated distinctly as a third lobe; metastylid present in later species. P^1 present, small in size; P^4 molariform with a bicusped ectoloph. Upper molars lack mesostyle; hypocone not strongly developed, absent in M^3; metaconule rudimentary or absent; strong external cingulum; internal cingulum continuous.

TYPE SPECIES. *Adapis parisiensis* (Blainville, 1841). Late Eocene (Late Ludian); France.

REMARKS. *Anchomomys*, *Pronycticebus*, and *Caenopithecus* differ from *Adapis* by having the M_3 hypoconulid more distinctly separated as a lobe and by lacking the bicusped ectoloph of P_4 and the continuous internal upper molar cingulum. *Caenopithecus* is further distinguished by lacking P^1 and having a mesostyle. In *Protoadapis* P_2 is much smaller than P_3 and the molar paraconids extend more internally. *Gesneropithex* has a median paraconid; the metaconid—protoconid crest is perpendicular to the longitudinal axis of the tooth and the M_2 trigonid is compressed antero-posteriorly.

The following species are referred to *Adapis:*

A. parisiensis (Blainville, 1841), p. 112, pl. 9. Late Eocene (Bartonian-Late Ludian); France.

A. magnus Filhol, 1874, p. 11, pl. 8, figs 9–12. Late Eocene (Bartonian-Early Ludian); France, Britain.

A. ruetimeyeri Stehlin, 1912, p. 1261, pl. 21, figs 5, 8, 12, 14. pl. 22, figs 17–19. Middle Eocene (Late Lutetian); Switzerland.

A. sciureus Stehlin, 1916, p. 1514, text-figs 368–370, pl. 22, fig. 5. Middle Eocene (Early Lutetian); Switzerland.

A. priscus Stehlin, 1916, p. 1511, text-figs 366–367. Middle Eocene (Early Lutetian); Switzerland.

Simons (1962) observed that the holotype of *Adapis minimus* Heller, 1930, is indeterminate owing to removal of enamel by post-mortem chemical absorption.

Adapis magnus Filhol, 1874

(Pl. 1; Pl. 2, fig. 1)

Diagnosis. Large size. Molars moderately elongated; metastylid developed. Upper canines large with grooved crown; P^3 transversely elongated with prominent internal cingulum and talonid.

Holotype. Fairly complete skull lacking the incisors and canines of both sides, left P^1–P^2 and M^3. ?Late Eocene/Early Oligocene (Quercy Phosphorites); Raynal, France. Described and figured, Filhol, 1874, p. 11, pl. 8, figs 9–12. Specimen not located.

Material. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

B.M. 30323. Fragment of right mandibular ramus with M_1–M_3. Very slightly worn. Brown shelly sand matrix. Listed, Lydekker, 1885a : 263.

B.M. 30856. Fragment of right mandibular ramus with M_2–M_3. Moderately worn. Brown sand matrix. Listed, Lydekker, 1885a : 263.

B.M. 29864. Fragment of right mandibular ramus with P_4–P_1, and posterior root of P_3. Moderately worn. Listed, Lydekker, 1885a : 263.

B.M. 29741. Fragment of left mandibular ramus with P_4, M_3, roots of P_3 and part of the canine. Teeth and alveoli of P_1–P_2 are badly damaged. External surface embedded in brown clayey sand matrix. Listed, Lydekker, 1885a : 263.

B.M. M10260. Fragment of left mandibular ramus with P_3–M_2 and alveoli of M_3. Fairly well worn.

B.M. M10269. Fragment of right mandibular ramus with P_4–M_2. Teeth unworn.

B.M. M10267 (3). Fragment of left mandibular ramus with M_1–M_2. Moderately worn.

D.M.S.W. M556 (41). Fragment of left mandibular ramus with P_4–M_2.

B.M. M26057 (1). Right M_2.
(2). Right M_1. Both teeth slightly worn. Wear and preservation indicates probable derivation from same individual.

B.M. M20560. Right M_2. Badly worn.

B.M. M25093. Left M_3. Badly damaged.

S.M. C30680. Fragment of right mandibular ramus with M_1–M_2. Slightly worn.

S.M. C53483. Left M_3. Unworn

S.M. C53477. Right M_3. Moderately worn.

S.M. C54221. Right M_2. Unworn.

S.M. C30659. Right M_1. Moderately worn.

S.M. C30660. Right M_1. Well worn.

S.M. C30656. Left M_2. Well worn.

S.M. C30658. Right M_2. Well worn.

S.M. C30657. Right M_1. Well worn.

S.M. C31345. Left M_2 (?). Well worn and badly damaged.

B.M. M3572. Fragment of left maxilla with left half of palate and P^2–P^3, M^1–M^3 and alveoli of the canine and P^1. P^2 is damaged. Teeth unworn. Listed, Lydekker, 1887 : 299.

B.M. M10261 (1). Left upper molar (M^2?). Moderately worn.
(2). Right upper molar (M^2?). Moderately worn.
(3). Upper molar. Moderately worn but badly damaged.
B.M. M20560 (1). Left upper molar (M^2?). Slightly worn.
(2). Left P^4. Moderately worn.
S.M. C53484. Left upper molar (M^3?). Unworn.
S.M. C30661. Right upper molar (M^2?). Slightly worn.
S.M. C30662. Right upper molar (M^1?). Slightly worn. Probably from same individual as S.M. C30661.
B.M. M25098. Right upper molar (M^2?). Unworn.
B.M. 25092. Right upper molar (M^1?). Moderately worn.
S.M. C53479. Left upper molar (M^3?). Moderately worn.
B.M. 12564 (1). Left upper molar (M^2?). Slightly worn.
(2). Right P^4. Moderately worn.
S.M. C30681. Right upper molar (M^3?). Well worn.
S.M. C30679. Left upper molar (M^1?). Badly worn.
S.M. C30673. Left upper molar (M^2?). Unworn.
S.M. C30674. Left upper molar (M^1?). Slightly worn. Probably from same individual as S.M. C30673.
S.M. C30678. Left P^4. Moderately worn.
S.M. C30675. Left upper molar (M^2?). Badly worn.
S.M. C30676. Right upper molar (M^2?). Slightly worn.
S.M. C30677. Fragment of upper molar.
B.M. 30346a. Listed, Lydekker, 1885a : 263.
(1) Right upper molar (M^2?). Slightly worn.
(2) Left upper molar (M^3?). Slightly worn. Probably from same individual as B.M. 30346a (1).
(3) Left P^4. Unworn.
(4) Left upper molar (M^3?). Unworn.
(5) Right upper molar (M^1?). Moderately worn but badly damaged.
(6) Left upper molar (M^1?). Unworn but slightly damaged.
(7) Left upper molar (M^2?). Unworn but slightly damaged. Probably from same individual as B.M. 30346a (6).
(8) Left upper molar (M^3?). Unworn.
(9) Left P^3. Slightly worn.
B.M. M25096. Right P^2. Slightly worn.
B.M. M10267. (1) Left P^2. Unworn.
(2) Right upper canine.

DESCRIPTION. The base of the strong coronoid crest and the shallow masseteric fossa are preserved in B.M. M10260. A small mandibular foramen occurs just below alveolar level. The posterior mental foramen lies between P_3 and P_4.

The lower incisors and P_1–P_2 are unknown from the Headon Beds. The lower canine is known (B.M. 29741) only by the root. P_3, preserved only in B.M. M10260, is oval and double-rooted, with an almost continuous cingulum; it has a main crested cusp which falls to a small anterior cusp and a single-cusped postero-internal talonid. P_4 (unworn in B.M. M10269) is moderately molarised with the protoconid larger than the metaconid. The metaconid is median and posterior to the protoconid. A slight swelling on the postero-internal wall of the metaconid (distinct in B.M. M10269 but indistinct in B.M. M10260) indicates a rudimentary metastylid. These cusps, which are crested transversely, form the oblique posterior trigonid wall. There are small external and antero-external cingula. A straight crest from the protoconid falls antero-basally to a small median paraconid which merges into a prominent antero-internal cingulum. From the prominent hypoconid, a crest runs antero-internally (crista obliqua) to meet the posterior protoconid wall, and internally to join a small but distinct entoconid (posterior to the hypoconid). A low crest from the entoconid runs anteriorly to the base of the metaconid. In B.M. M10260, the P_4 entoconid is vestigial.

In M_1, protoconid and metaconid are subequal when unworn. A metastylid is well differentiated, although it is indistinct in B.M. M10260; this cusp, with the crested paraconid and metaconid forms the strongly oblique posterior trigonid wall. From the protoconid a crest curves antero-internally to meet the paraconid external to the midline. This latter cusp, as in P_4, merges with a strong antero-internal cingulum. There are faint antero-external, external and postero-external cingula. The hypoconid is slightly larger than the more posteriorly situated entoconid; these cusps are joined by crests to a small but distinct median hypoconulid which is slightly posterior to the entoconid. There is a prominent crista obliqua. M_2 is closely similar to M_1, except for its larger size. The trigonid of M_3 is almost identical with that of M_1 and M_2, except for a generally poorly developed metastylid (in B.M. 30323 and B.M. 30856, for example). The hypoconid is strongly developed (as in M_1–M_2), with a prominent crista obliqua. The entoconid is vestigial (B.M. 30856) or represented by a low swelling (B.M. 30323) posterior to the hypoconid. The median hypoconulid (external to the midline in S.M. C53483) is as large as the hypoconid and surmounts a large rounded posteriorly projecting hypoconulid lobe which greatly extends the length of the talonid. From the hypoconulid, a low crest curves antero-internally, forming the internal talonid margin. The hypoconulid lobe is well separated from the hypoconid.

The upper canine alveolus (B.M. M3572) indicates a fairly large curved tooth. An isolated canine (B.M. M10267 (2)) has an almost continuous cingulum, more prominent internally. The tooth is grooved vertically on the anterior and posterior faces. P^1 is known from the Headon Beds only by an alveolus (B.M. M3572) indicating a very small single-rooted externally placed tooth. P^2 is oval and obliquely set in the tooth row (B.M. 25096) with an almost continuous cingulum which is strong generally except antero-externally. There is a large external anteriorly-crested cusp, and a small internal rounded lobe which is variably basined. P^3 is larger than P^2, with a large antero-external cusp and a smaller antero-internal cusp. The tooth is set obliquely in the jaw as in P^2. The antero-external cusp is crested anteriorly and posteriorly. There is a distinct parastyle which is connected to the protocone by a sharp crest. A cingulum is absent round the protocone but elsewhere it is prominent (although very reduced in B.M. 30346a (9)). P^4 is smaller than M^1 but larger and more quadrate than P^3, and set more squarely in the tooth row. The paracone is slightly larger than the metacone; these cusps are sharply crested anteriorly and posteriorly. The protocone and metacone are subequal. As in P^3, a sharp crest runs from the protocone to a distinct parastyle. The cingulum is generally well developed but absent anteriorly.

M^1 is roughly quadrate in outline and larger than P^4. Externally and anteriorly, the tooth is almost identical with P^4, except for a small paraconule midway along the protocone-parastyle crest and a stronger cingulum round the protocone base. There is a hypocone sited slightly internal to the protocone and opposite the metacone; this cusp, the smallest of the major cusps, is joined to the posterior cingulum by a low curved crest. M^2 is larger than M^1, but otherwise structurally nearly identical. M^3 is similar but slightly narrower antero-posteriorly than M^2. The M^3 internal

TABLE 13

Selected measurements (in mm) of *Adapis magnus*

	P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30323	—	—	—	—	6·8	5·1	7·4	5·4	9·3	5·0
B.M. 30856	—	—	—	—	—	—	7·6	5·4	9·4	4·7
B.M. 29864	—	—	6·4	4·8	7·1	5·1	—	—	—	—
B.M. M10260	6·3	4·0	7·1	4·4	7·0	4·8	7·6	5·3	—	—
B.M. M10269	—	—	6·8	4·8	6·9	5·7	7·2	6·1	—	—
B.M. M10267 (3)	—	—	—	—	6·7	5·0	7·3	5·4	—	—
D.M.S.W. M556 (41)	—	—	7·2	5·6	7·2	5·0	8·0	5·6	—	—
B.M. M26057 (1)	—	—	—	—	—	—	7·6	5·3	—	—
B.M. M26057 (2)	—	—	—	—	7·1	4·6	—	—	—	—
B.M. M25093	—	—	—	—	—	—	—	—	8·7	4·2
S.M. C54221	—	—	—	—	—	—	8·1	5·7	—	—
S.M. C53483	—	—	—	—	—	—	—	—	10·2	5·2
S.M. C53477	—	—	—	—	—	—	—	—	9·2	5·1

	P^3		P^4		M^1		M^2		M^3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 3572	4·7	5·8	—	—	6·7	7·4	7·0	8·8	7·0	8·8
B.M. M10261 (1)	—	—	—	—	—	—	6·9	8·3	—	—
B.M. M10261 (2)	—	—	—	—	—	—	7·0	8·3	—	—
B.M. M20560 (1)	—	—	—	—	—	—	7·5	8·3	—	—
B.M. M20560 (2)	—	—	6·2	7·5	—	—	—	—	—	—
B.M. M12564 (1)	—	—	—	—	—	—	6·3	8·1	—	—
B.M. M12564 (2)	—	—	6·1	7·2	—	—	—	—	—	—
S.M. C30678	—	—	6·4	7·5	—	—	—	—	—	—
S.M. C30674	—	—	—	—	7·5	9·7	—	—	—	—
S.M. C30679	—	—	—	—	6·9	8·3	—	—	—	—
S.M. C30681	—	—	—	—	—	—	—	—	7·0	8·8
S.M. C53479	—	—	—	—	—	—	—	—	7·0	7·5
S.M. C30662	—	—	—	—	6·6	7·6	—	—	—	—

cingulum in B.M. 30346a (2), is very rudimentary. In some specimens, the antero-internal molar cingulum is continuous with a crest from the hypocone; in other specimens this is not so. This feature is also variable in M^1–M^3 of the same individual, as in B.M. 3572.

REMARKS. The species has long been recognised from the Lower Headon Beds of Hordle Cliff. *Adapis magnus* (*sensu lato*) is subject to considerable variation and several distinct varieties have been recognised (Stehlin, 1912).

The species is distinguished from other species as follows: *A. sciureus* has shorter rounded molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid; P_3 is more simple and P_4 less molarised with a smaller talonid; the upper molars have a strong metaconule and protoconule and a stronger hypocone. *A. priscus* possesses rounded less elongated molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid. In *A. ruetimeyeri* the rounded molars lack a metastylid; the protoconid-metaconid crest is only slightly oblique and there is a strong hypocone. *A. parisiensis* is much smaller with the lower molars relatively more elongated antero-posteriorly; the upper molars are less extended transversely; P^3 is extended antero-posteriorly with a smaller internal cingulum and talonid, and the upper canine is smaller and lacks grooves.

Adapis parisiensis (Blainville, 1841)

(Pl. 2, figs 2, 3)

DIAGNOSIS. One third smaller than *A. magnus*, with molars relatively more elongated; metastylid variably developed. Upper canine small, generally lacking a grooved crown; P^3 elongated antero-posteriorly with small talonid and internal cingulum.

HOLOTYPE. A skull, according to Hill (1953), now in the Paris Museum. Late Eocene (Late Ludian); France. Described and figured, Blainville, 1841, p. 112, pl. 9 (Genus *Anoplotherium*).

MATERIAL. F.C.S. 7.

(1) Fragment of left mandibular ramus with M_1–M_3. M_3 is damaged.

(2) Fragment of right mandibular ramus with P_2–M_1, M_3, and alveoli of the canine, P_1 and M_2. Part of the symphysis is preserved.

(3) Right M_2–talonid only.

(4) Left P^2 (?).

(5) Left P^4 with roots embedded in a maxillary fragment.

(6) Left M^1 (?)—internal fragment with protocone only. All specimens from the same individual. Teeth moderately worn. Upper Headon Beds (Lignite Bed), Headon Hill.

DESCRIPTION. The mandible is fairly long. The posterior mental foramen lies below the posterior root of P_4; the larger anterior foramen is sited between the canine and P_1. A small intermediate foramen lies below the anterior root of P_2. The symphysis is long and oblique.

The canine alveolus indicates a semiprocumbent tooth. P_1 (from the alveolus) was small and single-rooted. P_2 is an oval double-rooted tooth with a large anteriorly crested cusp and a small postero-internally projecting talonid. The talonid bears a strong antero-posterior crest which posteriorly is raised into a small cusp. There is a fairly strong internal cingulum and a weak postero-external cingulum. P_3 is double-rooted and similar to P_2, except for a longer talonid and a larger talonid cusp. In P_4, the protoconid and metaconid appear to be subequal but this is obscured by wear on the one specimen. The metaconid is markedly posterior to the protoconid, with a distinct postero-internal metastylid. A straight anterior protoconid crest joins a distinct median paraconid. There is a strong antero-internal shelf-like cingulum and a smaller continuous antero-external, and postero-external cingulum. The hypoconid is joined to the smaller more posteriorly sited entoconid by a curved posterior crest, and joined to the posterior trigonid wall by a strong crista obliqua.

M_1 is almost identical with P_4, except that the entoconid and hypoconid are subequal, and there is a small median hypoconulid slightly posterior to the entoconid. M_2 differs from M_1 only by its larger size. M_3 is very similar but broader and more elongated antero-posteriorly than the other molars; the metastylid is very well developed, being higher when unworn, than the protoconid. The talonid is almost the same as in *A. magnus:* the moderately developed hypoconid is joined to the posterior trigonid wall by an oblique crest; the smaller entoconid is slightly posterior to the hypoconid; the hypoconulid, the largest talonid cusp is extended posteriorly as a prominent rounded median separated lobe.

P^1 is ovoid with a large external cusp which is crested anteriorly and posteriorly; internally the tooth is basined. There is a strong cingulum except externally where it is vestigial. P^4 is slightly elongated transversely. Of the major cusps, the protocone appears to be the largest and the metacone smallest, with the paracone intermediate in size. The paracone and metacone are crested anteriorly and posteriorly. A strong broad crest runs from the protocone to a distinct parastyle. A strong external and posterior cingulum is present. Antero-internally there is a short cingulum; this does not extend round the protocone base. Postero-internally there is little sign of a hypocone differentiated from the cingulum. The M^1 internal fragment shows a strong cingulum which is continuous round the protocone base and a small distinct hypocone.

REMARKS. Distinguished from other species as follows: *A. sciureus* has rounded shorter lower molars; the protoconid-metaconid crest is only slightly oblique and there is no metastylid; P_3 is more simple; P_4 is less molarised with a smaller talonid, and the upper molars have a strong metaconule and protoconule, with a stronger hypocone. *A. priscus* possesses rounded less elongated lower molars; the protoconid-metaconid crest is slightly oblique and there is no metastylid. In *A. ruetimeyeri*, the rounded lower molars lack a metastylid; the protoconid-metaconid crest is slightly oblique and the upper molar hypocone is strong. The presence of P_1, the strongly oblique protoconid-metaconid crest and a prominent metastylid, support reference of this specimen to *A. magnus* or *A. parisiensis*. However, *A. magnus* is much larger and has relatively less elongated lower molars and a slightly more transverse protoconid-metaconid crest.

There is considerable variation in the skull, posterior region of the mandible and molars of *A. parisiensis*. Filhol (1883) recognised six varieties which were reduced to three by Stehlin (1912 : 1235). F.C.S. 7 does not agree closely with any of Stehlin's figured specimens, differing in the greater development of the metastylid and in mandible shape. The material is perhaps best considered as a variety of *A. parisiensis;* it is undoubtedly specifically distinct from *A. magnus* from the Lower Headon Beds.

TABLE 14

Measurements (in mm) of *Adapis parisiensis*

	P_2		P_3		P_4		M_1		M_2		M_3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
F.C.S. 7 (1)	—	—	—	—	—	—	6·1	4·1	6·6	4·5	8·7	4·0
F.C.S. 7 (2)	4·7	3·0	5·0	3·2	5·6	4·0	5·9	4·2	—	—	8·6	4·8

Family **TARSIIDAE** Gray, 1825

DIAGNOSIS. Zygomatic arches slender. Brain case much expanded transversely. Bullae much inflated; ectotympanic tubular, extends out of bulla. Foramen magnum directed largely downwards. Very short narrow muzzle; palate narrow anteriorly. Tooth rows converge (V-shaped). Upper canine smaller than anterior incisor. Lower canine larger than upper. Hypocone often small. (after Simons, 1961).

REMARKS. Following Simons (1961), the group is divided into two subfamilies:

Tarsiinae Gray, 1825. Recent; East Indies–Philippines.

Microchoerinae Lydekker, 1887. Middle-Late Eocene; Europe.

On the basis of relationship with *Tarsius*, Simons (1961 : 53) placed the Microchoerinae (previously grouped with the Anaptomorphidae) in the Tarsiidae. Following McKenna (1967) and Russell, Louis & Savage (1967), Microchoerinae Lydekker, 1887 is adopted in preference to the previously more widely used Necrolemurinae Simpson, 1940.

Subfamily **MICROCHOERINAE** Lydekker, 1887

DIAGNOSIS. Skull with comparatively large anteriorly-directed orbits. Snout reduced in size with anterior convergence of the tooth rows. Typically the dental formula is $\frac{2}{0}, \frac{1}{1}, \frac{3}{4}, \frac{3}{3}$, with total loss of lower incisors except in one species. Lower canine enlarged and P_1 small and vestigial. Upper canine small and premolariform, the upper enlarged tooth being the most anterior incisor, here considered as I^2. P_4 not elevated, having a short heel and tending towards a molariform condition.

P_2–P_4 low and oval in shape. In M_2–M_3, paraconid fusing with metaconid, the talonid basined and subovate. Upper molars quadrate with large hypocone usually developed on border of a postero-internal basin. Metaconule and protoconule developed and in more advanced forms, numerous accessory cuspules. (compiled from Simpson, 1940, and Simons, 1961).

Remarks. Distinguished from the other subfamily as follows: The Tarsiinae has upper molars with a primitive tritubercular crown, a rudimentary hypocone and a reduced metaconule.

Five genera are currently referred to the Microchoerinae:

Microchoerus Wood, 1884. Late Eocene; Britain, France, Switzerland, Spain.
Necrolemur Filhol, 1873. Middle-Upper Eocene; France, Germany.
Nannopithex Stehlin, 1916. Middle Eocene; Switzerland.
Pseudoloris Stehlin, 1916. Late Eocene; France, Spain.
Agerina Crusafont, 1967. Middle Eocene; Spain.

Microchoerus and *Necrolemur* have long been placed in this subfamily. Recent work by Hürzeler (1948) and Simons (1961 : 61) has added *Nannopithex*, previously only tentatively assigned to the group. Simons has also shown (1961 : 54) that *Pseudoloris*, formerly placed by Simpson (1940 : 198) in the Anaptomorphidae as the single member of a separate subfamily, is closely related to the three former genera and should be placed, therefore, in the Microchoerinae. The genus *Periconodon* from the Middle Eocene of Switzerland, was tentatively assigned to the group by Hill (1955 : 290), but Simons (1962 : 30) referred it to the Omomyidae; more recently, this genus has been placed tentatively in the Adapidae by Russell, Louis & Savage (1967). Crusafont (1967) departed from the generally accepted classification by referring *Pseudoloris* to the Omomyidae.

Genus ***MICROCHOERUS*** Wood, 1844

Diagnosis. Upper molars with hypocone, mesostyle and numerous accessory cuspules; M_3 with a prominent wide rounded posterior lobe, separated from hypoconid and entoconid by small constrictions; small though distinct paraconid on M_1, not distinct on M_2 and M_3. Extensive enamel crenulations on lower molars.

Type species. *Microchoerus erinaceus* Wood, 1844. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

Remarks. Distinguished from other genera as follows: *Pseudoloris* is much smaller with sharp cusps; the molars lack enamel crenulation and accessory cuspules; upper molars lack a mesostyle; the lower molars have a distinct paraconid and the M_3 hypoconulid lobe is narrow, sharp and well separated. *Nannopithex* is smaller with only slight enamel crenulation; no mesostyle is developed and the M_3 hypoconulid lobe is narrower and more distinctly separated. *Necrolemur* has only slight enamel crenulation in the molars and lacks a mesostyle, and the M_3 hypoconulid lobe is less developed.

Three species have been described:

M. erinaceus Wood, 1844, p. 350. Late Eocene (Early Ludian); Britain, France, Spain.

M. edwardsi (Filhol, 1880), p. 124. Late Eocene (Late Ludian); Britain, France.

M. ornatus Stehlin, 1916, p. 1377, pl. 22, fig. 12. Late Eocene (Late Ludian); Switzerland, Spain.

M. erinaceus and *M. edwardsi* are known from parts of the maxillae and fragmentary mandibles; *M. ornatus* is based on a partial upper dentition.

Crusafont (1967) considered that *Microchoerus edwardsi* was synonymous with *M. erinaceus*. In the same work, Crusafont (1967) referred *Microchoerus erinaceus* to *Necrolemur* and considered *Necrolemur antiquus* Filhol as a synonym of '*Necrolemur*' *erinaceus; Microchoerus* (*sensu stricto*) was retained for the species *M. ornatus*.

Microchoerus erinaceus Wood, 1844

(Pl. 3; Pl. 4)

Diagnosis. Dental formula $\frac{2}{0}, \frac{1}{1}, \frac{3}{4}, \frac{3}{3}$. The largest species. Apparently lacks lower incisors. Upper molars only moderately complex, lacking duplicated paraconule. P^3 with rounded outline and a single large external cusp.

Holotype. B.M. 25229 (1). Fragment of left mandibular ramus with P_4–M_3. (2) Palatal fragments with an almost complete dentition, lacking only the left canine and right I^2 (latter tooth reconstructed in plaster). Fairly badly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. Listed and described, Wood, 1844 : 350; Figured, Wood, 1846 : 12, figs 1 and 3; Described and figured, Lydekker, 1885d : 529, fig. (unnumbered); Figured (upper), Lydekker, 1887 : 304, fig. 45; Described and figured, Cooper, 1910 : 40, pl. 3, fig. 1; Described and figured, Simons, 1961 : 59, fig. 2.

Material. All specimens from the Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where stated otherwise.

B.M. 10768. Fragment of right mandibular ramus with M_1–M_3. Fairly badly worn; crowns damaged.

B.M. M12563 (1). Fragment of left mandibular ramus with P_4–M_2.
(2). Fragment of right mandibular ramus with M_1–M_3.
(3). Isolated M_3, probably from (1) above.

B.M. 30346. Fragment of left mandibular ramus with M_1–M_2.

B.M. 30346b (1). Fragment of left mandibular ramus with M_2 and broken M_1.
(2). Fragment of right mandibular ramus with M_3.
(3). Fragment of left mandibular ramus with P_4–M_3.
(4). Fragment of right maxilla with M^1–M^3.
(5). Right M^2.
(6). Right P^4.

Mentioned by Lydekker, 1887, p. 304. (4) above, listed Cooper, 1910 : 40.

B.M. M2605b. Isolated M_1, M_2 and M_3, from same individual.

S.M. C9672. Left mandibular ramus with M_1–M_3. Posterior region almost complete. Listed and figured, Cooper, 1910 : 39; pl. 3, fig. 6.

S.M. C9681. Left mandibular ramus with P_3–M_3 and the alveoli of the canine, P_1 and P_2. The symphysis is preserved.

S.M. C9670. Left mandibular ramus with P_2–M_3. Listed and figured, Cooper, 1910 : 40; pl. 3, fig. 4.

S.M. C9671. Right mandibular ramus with P_3–M_3 and roots of the canine, P_1 and P_2. Symphysis preserved. Listed, Cooper, 1910 : 39. According to Cooper, associated with S.M. C9670.

S.M. C9673. Fragmentary right mandibular ramus with M_1–M_2, damaged M_3 and roots of P_4. Listed, Cooper, 1910 : 40.

S.M. C9675. Fragmentary right mandibular ramus with P_4–M_2.

S.M. C9678. Right M_3.

S.M. C9679. Right M_2. Probably from same individual as S.M. C9678.

S.M. C9680. Fragment of right mandibular ramus with P_4 and M_1. Probably from same individual as S.M. C9678.

S.M. C54174 (1). Right P_3. Unworn, slightly damaged.
(2). Left M_1. Talonid only. Almost unworn. Lower Headon Beds (Rodent Bed), Hordle Cliff.

S.M. C53482. Fragment of left mandibular ramus with roots of P_4, M_1, and alveoli of the canine and P_1–P_3.

B.M. M26055. Fragment of left mandibular ramus with P_2–M_3. P_3 damaged. Teeth badly worn. Upper Headon Beds (*Microchoerus* Bed), Headon Hill.

F.C.S. 3. Left M_3. Upper Headon Beds (Lignite Bed), Headon Hill.

B.M. M12563 (1). Right M^2.
(2). Left M^1.

S.M. C9669. Palatal fragment with right and left M^2–M^3. Listed, Cooper, 1910, p. 39.

S.M. C30710–27. Teeth mounted on a board:
S.M. C30712. Left M^2.
S.M. C30714. Left M^2.
S.M. C30715. Left M^1.
S.M. C30716. Right M_1.
S.M. C30717. Right M_2.
S.M C30718. Left M^1.
S.M. C30719. Right P^4.
S.M. C30720. Left P^4.
S.M. C30723. Left M_1.
S.M. C30724. Right M_2.
S.M. C30727. Right upper canine.

B.M M12565a (1). Right M_1.
(2). Right M_1 (or M_2).
(3). Right M^1.

(4). Right I^2 (?).
(5). Right upper canine (?).
B.M. M12565c (1). Left upper canine (?).
(2). Right P^3. Partially embedded in matrix.
B.M. M25090 (1). Left I^2 (?).
(2). Left I^3 (?). Both moderately worn.
S.M. C54175 (1). Left P^3. Moderately worn.
(2). Left upper canine (?). Lower Headon Beds (Rodent Bed), Hordle Cliff.

DESCRIPTION. The mandible is fairly short and stout; the oval-shaped symphysis (S.M. C9681, S.M. C9671, and S.M. C9670) is steeply inclined, following the line of the canine root. Below P_3, the lower edge of the mandible projects internally as a small shelf. The smaller posterior mental foramen lies below P_4 (S.M. C9671) and S.M. C9681), or slightly anterior to this (S.M. C9670 and S.M. C53482). The position of the larger anterior mental foramen varies from below P_3 (S.M. C9671 and S.M. C9681) to below P_2 (S.M. C9670). The posterior region is preserved only in S.M. C9672 (wax restoration of the type excepted). The moderately developed rounded angular process falls considerably below the lower anterior margin of the mandible. The mandibular foramen lies just below alveolar level. The coronoid is small, the posterior margin rather damaged on the specimen. The slender condyle has an articulating surface which is slightly elongated transversely; it lies considerably above the tooth row level. The coronoid crest is more prominent than the condyloid crest, although both are not well developed.

The tooth row is compact and continuous. In M_3 the protoconid and metaconid are subequal and larger than the hypoconid and entoconid. A small crest which unites the protoconid and metaconid follows the rounded anterior tooth margin; there is no distinct cuspate paraconid. A crest from the hypoconid runs antero-internally towards the metaconid. The posterior region of the talonid is separated into a prominent rounded hypoconulid lobe which is slightly displaced internally; this lobe greatly increases the length of the talonid. In B.M. 10768, the hypoconulid lobe is considerably enlarged relative to the other specimens. There is no distinct cuspate hypoconulid but the lobe bears an internal and an external accessory cusp; these accessory cusps are rather indistinct in some specimens especially after wear. There is a fairly strong external cingulum (only weakly developed in S.M. C9672). Several specimens show slight traces of an internal cingulum.

M_2 is more quadrate than M_3 but otherwise very similar without the hypoconulid lobe. No paraconid is distinguishable as in M_3; the protoconid, metaconid and hypoconid are subequal in size, the entoconid smaller. There is a small bilobed median hypoconulid on the hypoconid-entoconid crest (indistinct on S.M. C9681). In most specimens, there is an accessory cuspule (mesoconid) on the prominent crista obliqua. A strong external cingulum is present (weak in S.M. C9672) but there is no trace of an internal cingulum.

M_1 is similar structurally to M_2, with a small duplicated hypoconulid on most specimens (not distinguishable on S.M. C9671) and a mesoconid. There is no internal cingulum. The tooth differs from M_2 and M_3 by having a more squared anterior margin and a small distinct paraconid situated directly anterior to the metaconid; the paraconid is separated from the metaconid but united to the protoconid by a low crest.

P_4 is smaller and subtriangular with a small low heel. The tooth is dominated by a large median protoconid. A curved antero-basally directed crest from the protoconid forms the anterior tooth margin; the posterior face of the protoconid bears two crests. The smaller separated metaconid in S.M. C9680, S.M. C9670, S.M. C9671 and S.M. C9675 is more posteriorly placed than the protoconid and falls to a strong antero-internal cingulum. In the holotype (B.M. 25229) and S.M. C9681, the protoconid and metaconid are opposite and the internal cingulum is only weakly developed. S.M. C9681 and S.M. C9670 have a well developed external cingulum; this is poorly developed in S.M. C9680, S.M. C9674 and S.M. C9681.

P_3 (well preserved in S.M. C9681, S.M. C9671 and S.M. C9670) bears a large median anteriorly crested cusp and a small cingulum-like heel; there is a strong internal cingulum. In S.M. C9671 and S.M. C9670 the anterior crest runs parallel to the length of the tooth; the main cusp slopes moderately basally towards the heel, bounded by two sharp crests; an external cingulum is moderately developed. In S.M. C9681, the anterior crest curves round towards the internal cingulum; the main cusp is more posteriorly situated, falling more steeply to the heel and the two posterior crests are less prominent.

P_2 (S.M. C9670 and B.M. M26055) is made up of an anteriorly-crested cusp and a small cingulum-like heel. The cusp is concave internally and convex externally. There is a prominent internal cingulum and a smaller external cingulum.

P_1, represented only by an alveolus (S.M. C9681) and a broken root (S.M. C9671) was evidently a small anteriorly inclined tooth, situated on the external edge of the tooth row. The broken root (S.M. C9671) and a large oval deep alveolus (S.M. C9681) of the lower canine indicate a large anteriorly-inclined tooth, lying at a much lower level in the jaw than the other teeth.

I^2–P^4 are associated only in the holotype. The most anterior tooth I^2, is enlarged with almost vertical sides. I^3 is considerably smaller with an antero-internally sloping crown and a small external cingulum. The semi-procumbent canine is much enlarged (but not as high as I^2) and has an external cingulum. P^2 is single-rooted and semi-procumbent with a small heel; the tooth is smaller than the canine.

P^3 and P^4 are quadrate and larger than P^2; both have a single large external cusp and a strong external cingulum. P^4 has a small antero-internal and a small postero-internal cusp which are sharp and unworn in S.M. C30719 and S.M. C30720; these are worn down to an antero-posterior ridge in the holotype and B.M. 30346b (6).

M^1 and M^2 are quadrate and subequal in size; the metacone lies on a straight antero-posterior line with the paracone. In the smaller M^3, with a more rounded posterior margin, the metacone is more internal to the paracone. The hypocone, which in M^1 is almost equal to the protocone, becomes progressively smaller in M^2 and M^3. A paraconule and metaconule are well developed in all molars, the former sited anterior of a line between protocone and paracone, the latter anterior of a line between metacone and hypocone. The metaconule, equal to the paraconule in M^1, becomes progressively smaller in M^2 and M^3. In all molars, a small accessory cusp is situated midway between the metaconule and the protocone; this can be regarded as a duplication of the metaconule. In M^1 and M^2, this accessory cusp is smaller than the main metaconule, but in M^3 it is larger. There is a prominent mesostyle in M^1 and M^2 external to a line between the paracone and metacone. This cusp is represented in M^3 by a slight cingular swelling. A small but definite hypostyle occurs on M^1 and M^2 of B.M. 30346b (4). A parastyle and metastyle are encountered more frequently, appearing as upgrowths from the prominent external cingulum: a parastyle occurs on M^2 of S.M. C30712 and S.M. C30714 and M^1 of B.M. 30346b (4), B.M. M12563 (2), S.M. C30715 and S.M. C30718; the metastyle is present on M^2 of the holotype (B.M. 25229), B.M. 30346b (4), S.M. C30712 and S.M. C30714 and the M^1 of B.M. 25229 and B.M. 30346b (4). In all other specimens, these three accessory cusps are indistinct.

Remarks. The number of specimens is really inadequate for any satisfactory statistical treatment of variation within the species to be carried out. However, some tentative conclusions may be drawn from the available material. The following variates were considered: length and width of M_3, M_2, M_1 and P_4; length of tooth rows M_1–M_3 and P_4–M_3 and the internal depth of the mandible below the posterior

Table 15

Selected measurements (in mm) of *Microchoerus erinaceus*

	P_2		P_3		P_4		M_1		M_2		M_3		M_1–M_3
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. 25229 (1)	—	—	—	—	3·0	2·8	4·2	3·6	—	(3·4)	4·3	3·0	11·0
B.M. 10768	—	—	—	—	—	—	(2·5)	(2·9)	3·8	3·2	4·5	2·7	—
B.M. M12563 (1)	—	—	—	—	3·0	2·6	4·1	3·9	4·2	3·9	—	—	—
B.M. M12563 (2)	—	—	—	—	—	—	4·2	3·7	4·3	3·6	4·8	3·2	—
B.M. 30346	—	—	—	—	—	—	4·6	3·4	4·9	3·4	—	—	—
B.M. M26055	3·4	2·1	—	2·4	3·4	2·7	4·3	3·2	4·0	3·0	4·4	2·8	—
S.M. C9670	3·0	2·2	3·1	2·3	3·5	2·8	3·7	3·4	3·7	3·4	4·5	3·0	11·8
S.M. C9671	—	—	3·1	2·3	3·3	2·9	3·8	3·5	3·7	3·4	4·6	3·1	11·9
S.M. C9681	—	—	3·1	2·4	3·4	2·9	4·2	3·5	3·9	3·4	4·2	2·5	12·0
S.M. C9672	—	—	—	—	—	—	4·1	4·0	4·0	3·5	4·6	3·0	12·5
S.M. C9673	—	—	—	—	—	—	4·0	3·2	4·0	3·2	—	—	—
S.M. C9675	—	—	—	—	3·5	3·0	4·3	3·9	4·4	3·7	—	—	—

	P^2		P^3		P^4		M^1		M^2		M^3	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 25229 (2)	—	—	2·9	3·5	3·1	3·8	4·0	4·6	3·6	5·0	3·0	3·9
B.M. 25229 (2)	2·9	2·4	2·7	3·5	3·0	4·2	4·0	4·7	3·9	4·9	3·2	4·0
B.M. 30346b (4)	—	—	—	—	—	—	4·2	5·0	4·0	4·9	2·8	4·0
B.M. 30346b (5)	—	—	—	—	—	—	—	—	4·1	4·7	—	—
B.M. 30346b (6)	—	—	—	—	3·4	3·8	—	—	—	—	—	—
B.M. M12563 (1)	—	—	—	—	—	—	—	—	3·9	5·1	—	—
B.M. M12563 (2)	—	—	—	—	—	—	4·2	4·9	—	—	—	—
S.M. C9669	—	—	—	—	—	—	—	—	3·9	(4·8)	3·1	4·2
S.M. C9669	—	—	—	—	—	—	—	—	3·8	5·0	3·0	4·2
S.M. C30715	—	—	—	—	—	—	—	4·4	—	—	—	—
S.M. C30719	—	—	—	—	—	3·8	—	—	—	—	—	—
S.M. C30720	—	—	—	—	—	3·4	—	—	—	—	—	—

margins of M_3, M_1 and P_3. The mandible depth in *M. erinaceus* appears to be highly variable and cannot be correlated with individual age as reflected by dental wear. Frequency distributions utilising dimensions of the posterior lower teeth indicate a separation of the larger specimen B.M. 30346; this is removed by secondary grouping of the data and is, in all probability, due only to incomplete sampling. P^3–P^4 of the type specimen (B.M. 25229 (1)) and S.M. C9681 are different structurally from the rest of the material. These differences might be sexual or could possibly indicate an anterior milk dentition; they are unlikely to be of specific importance.

Simons (1961) observed an alveolus anterior to the lower canine in some French specimens of *M. edwardsi*, indicating at least one lower incisor. There is no evidence for similar teeth in the specimens of *M. erinaceus* from the Headon Beds. But preservation of this region of the mandible is rare and their absence in *M. erinaceus* should be treated with caution. Apart from the probable structural difference in dentition, *M. erinaceus* differs from *M. edwardsi* by its greater size.

Several features of the upper dentition distinguish the species from *M. ornatus* (known only from upper dentition): P^3 in *M. erinaceus* has a rounded outline and a single major external cusp whilst this tooth in *M. ornatus* has a squared outline and two external cusps. In addition to the duplicated metaconule present in both species, the M^2 of *M. ornatus* is further complicated by a duplicated paraconule and a prominent hypostyle. *M. erinaceus* is significantly larger than *M. ornatus*: in the holotype of *M. erinaceus*, the length of the tooth row, M^2–M^3 is 11·0 mm, whereas in the holotype of *M. ornatus*, this measurement is 9·0 mm.

Genus ***PSEUDOLORIS*** Stehlin, 1916

DIAGNOSIS. Small size. No accessory cuspules and enamel crenulations. Upper molars relatively elongated transversely, lacking mesostyles; cingulum-hypocone distinct on M^1 and M^2, indistinct on M^3; lower molar cusps relatively sharp and separated. M_3 entoconid and hypoconulid high and separated with distinct narrow hypoconulid-lobe. Distinct small paraconid on M_1 and M_2, reduced on M_3.

TYPE SPECIES. *Pseudoloris parvulus* (Filhol, 1890). ? Late Eocene (Quercy Phosphorites); France.

REMARKS. The genus was proposed by Stehlin (1916 : 1397) for a species originally described by Filhol, (1890a) as *Necrolemur parvulus*. The validity of this genus has been subsequently accepted generally.

Simpson (1940 : 198) agreeing with Teilhard de Chardin (1916–1921a) that *Pseudoloris* was significantly *Tarsius*-like, erected a new subfamily, Pseudolorisinae, for this monospecific genus. Recently Simons (1961 : 54) has shown that the similarities between *Pseudoloris* and other microchoerines are so great, that separation at subfamily level is not possible.

Weigelt (1933) described *P. abderhaldeni* from the Middle Eocene brown coal deposits of Geiseltal, Germany. Simons (1961 : 61) stated that the type of this species is conspecific with '*Necrolemur*' *raabi* Heller, the latter species being referable to *Nannopithex*. Crusafont (1967) described a new species, *Pseudoloris reguanti* from the Upper Ludian of Spain.

Pseudoloris is distinguished from other genera as follows: *Microchoerus* has a mesostyle and is markedly larger with lower rounded cusps; the M_3 hypoconulid-lobe is wide and rounded and the molars possess numerous accessory cuspules and enamel crenulations. In *Necrolemur* the M_3 hypoconulid-lobe is wide and rounded; the cusps are lower, rounded and less distinct and the genus is much larger. *Nannopithex* has slight enamel crenulations in all teeth; P_4 is much larger than the lower molars; the molar cusps are more rounded and lower, and M_3 entoconid and hypoconulid are not as high and separated.

Pseudoloris parvulus (Filhol, 1890)

(Text-fig. 23)

1890 *Necrolemur parvulus* Filhol.

DIAGNOSIS. As for genus.

HOLOTYPE. Fragment of left mandibular ramus with P_3–M_3 and alveoli of the canine, P_1–P_2. ?Late Eocene (?Ludian, Quercy Phosphorites); Caylux, France. Described and figured, Filhol (1890a : 39, text-fig., unnumbered). Specimen not located by Teilhard de Chardin (1916–1921a : 5). Abundant referred material described and figured by Stehlin (1916 : 1397) and Teilhard de Chardin (1916–1921a : 4).

MATERIAL. B.M. 36812f. Fragment of right mandibular ramus with M_2–M_3. Teeth slightly worn. Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff.

DESCRIPTION. M_2 and M_3 are elongated antero-posteriorly. The trigonid and basined talonid are well differentiated, but the cusps are low, the trigonid cusps being only slightly higher than those of the talonid.

In M_2, the trigonid and talonid are subequal in width but the trigonid is compressed antero-posteriorly and is shorter. The protoconid is slightly higher than the metaconid and markedly more anteriorly placed; both cusps are crested transversely. The metaconid is internal in position; the protoconid tip lies just external to the longitudinal midline. There is a well developed antero-external cingulum. A small median cuspate paraconid forms the sharp anterior trigonid apex; this cusp is joined by a small low crest from the metaconid and from the protoconid. The talonid is strongly basined. The entoconid is slightly smaller than the metaconid; a sharp crest runs anteriorly from the entoconid to meet, at the base of the posterior trigonid wall, a sharp metaconid crest. Although the tooth is damaged externally, it appears that the hypoconid was opposite, or just anterior to the entoconid, a strong crista obliqua running from this cusp to the base of the posterior protoconid wall. A rudimentary hypoconulid is represented as a very small projection on the posterior talonid margin, just external to the midline; this is joined to the hypoconid and entoconid by small crests. Owing to damage, the extent posteriorly of the cingulum cannot be observed; it may have been continuous round the base of the hypoconid as in M_3.

The anterior part of M_3 is very similar to that of M_2, differing only in minor features: the protoconid is slightly more externally placed, and is subequal with the metaconid; the posterior trigonid margin is less oblique than in M_2 and the paraconid is slightly less developed and more crestiform in appearance, forming a more rounded anterior trigonid apex. The anterior part of the talonid is also very similar. M_3 differs markedly from M_2 by having a hypoconulid-lobe. This long prominent separated lobe is narrow and mainly median although the posterior extremity is slightly internally directed. The lobe, consisting of a single large crestiform cusp, is connected with the hypoconid and entoconid by crests. A prominent continuous antero-external, external and postero-external cingulum is present.

REMARKS. Recently *Pseudoloris parvulus* has been recorded by Crusafont from the Early Ludian of Sosis, Spain (1965, 1967) and Euzet-les-Bains, France (1967). The single specimen from the Headon Beds appears to agree precisely with additional material of *Pseudoloris parvulus* figured by Stehlin (1916), Teilhard de Chardin (1916–1921a) and Piveteau (1957); it constitutes the first record of the genus from the Early Ludian of Britain.

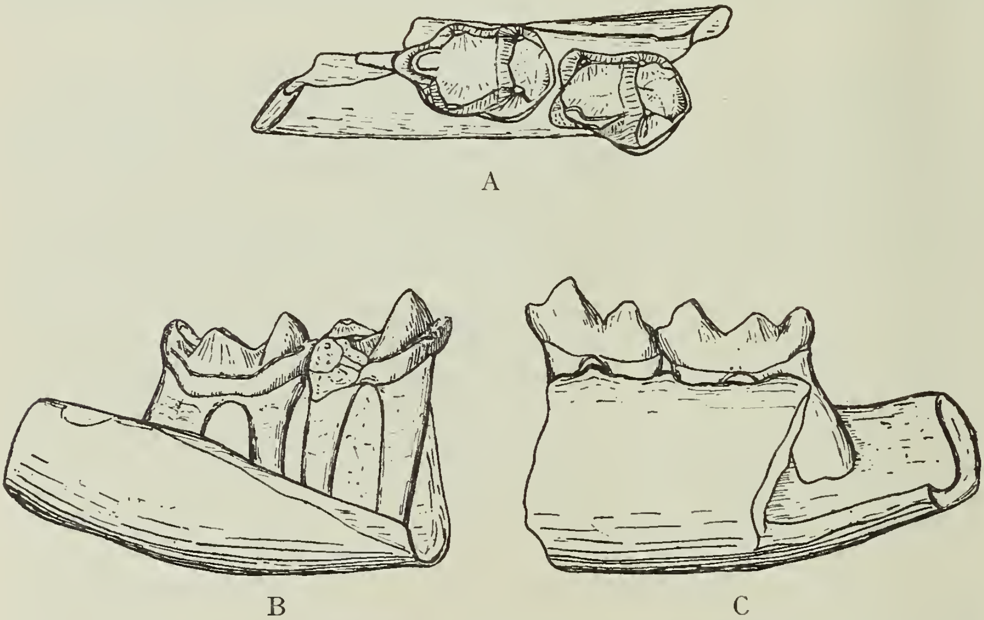

FIG. 23. *Pseudoloris parvulus* (Filhol, 1890). Fragmentary right mandibular ramus with M_2–M_3. B.M. 36812f ×12. Lower Headon Beds, Hordle Cliff. (A) Occlusal view. (B) External view. (C) Internal view.

TABLE 16

Measurements (in mm) of *Pseudoloris parvulus*

	M_2		M_3	
	a-p	trs	a-p	trs
B.M. 36812f	1·6	1·25	1·9	1·2

Order CREODONTA

Family **HYAENODONTIDAE** Leidy, 1869

DIAGNOSIS. $P\frac{1}{1}$ double-rooted except in some specialized genera; P^3 lacking distinct protocone; $M\frac{1}{2}$ or $M\frac{2}{3}$ functioning as main carnassials; $M\frac{3}{3}$ present or absent; cheek teeth row moderate to long; $M\frac{3}{3}$ when present transversely extended. Jaw long and shallow to moderately short and deep, with symphysis weak to fairly robust, and angle long, slender, projecting and upcurved at tip. Face long to moderately short; basicranial region narrow to moderately wide; no preglenoid crest (mainly from Denison, 1938 : 117).

REMARKS. The order Creodonta is retained here in a restricted sense, following Romer, (1966 : 229). The family is known from the Early Eocene-Middle Oligocene of North America; Early Eocene-Late Oligocene of Europe; Late Eocene-Oligocene, Early Pliocene of Asia and the Early Oligocene, Early Miocene of Africa.

Denison (1938) distinguished four subfamilies: Proviverrinae, Hyaenodontinae, Limnocyoninae and Machaeroidinae; this was followed by Simpson, (1945). Gazin (1946) proposed a new family, Limnocyonidae, to accommodate the latter two subfamilies. Van Valen (1966) placed all four subfamilies in the Hyaenodontidae but reduced them to the rank of tribes; Gazin's two fold subdivision was retained as two subfamilies, the Hyaenodontinae and the Limnocyoninae. More recently, Van Valen (1967) has abandoned the use of tribes within the Hyaenodontinae, grouping together the Hyaenodontini and the Proviverrini. In the present work, the earlier scheme of Denison is utilized as it provides a simple working arrangement (see also Savage, 1965).

Subfamily **HYAENODONTINAE** Trouessart, 1885

DIAGNOSIS. Long faced, narrow skulled genera; main carnassials $M\frac{2}{3}$ with carnassial specialization very advanced; M_3 present, M^3 variably present or absent; molars sectorial, length greater than width; M^3, where present, small and transverse; M^1 and M^2 with paracone and metacone completely or nearly connate and protocone reduced or absent; lower molars lack metaconid, talonid vestigial or absent. Body compact, robust; limbs and feet cursorial (after Matthew, 1909 and Savage, 1965).

Remarks. Distinguished from the other subfamilies as follows: in the Proviverrinae, the metaconid is retained; the carnassial specialization is less advanced and M_3^3 are invariably present. The Limnocyoninae and Machaeroidinae both have M_2^1 functioning as the main carnassials. Savage (1965) listed five good genera in the Hyaenodontinae:

Hyaenodon Laizer & Parieu, 1838. Late Eocene-Late Oligocene; Europe. Late Eocene-Middle Oligocene; North America, Asia. Early Oligocene, Early Miocene; Africa.
Pterodon Blainville, 1839. Late Eocene-Early Oligocene; Europe. Late Eocene-Early Oligocene; North America. Early Oligocene, Early Miocene; Africa. Late Eocene; Asia.
Apterodon Fischer, 1881. Early-Middle Oligocene; Europe. Early Oligocene; Africa.
Metapterodon Stromer, 1926. Early Miocene; Africa. Early Oligocene; Europe.
Leakitherium Savage, 1965. Early Miocene; Africa.

Simpson (1945) listed *Hemipsalodon* Cope, 1885; *Dasyurodon* Andreae, 1887 and *Propterodon* Martin, 1906. Savage (1965) has considered that *Hemipsalodon* is a synonym of *Pterodon* and *Dasyurodon* a synonym of *Apterodon*. More recently, Van Valen (1966 and 1967) has asserted the generic validity of *Hemipsalodon* and has stated (1967) that *Metapterodon* is a synonym of *Pterodon*; he also adds *Ischnognathus* Stovall, 1948 (Van Valen, 1966 and 1967) and (tentatively) *Hyainailouros* Biedermann, 1863 (Van Valen, 1967). *Propterodon* is not well known (see Van Valen, 1966 : 75) and Savage has stated (personal communication) that this latter genus will probably prove to be invalid. According to Van Valen (1967), *Megalopterodon* Dashzeveg, 1964, is synonymous (provisionally) with *Pterodon*. *Apterodon* was referred by Van Valen (1966) to the Mesonychidae; the genus was returned to the Hyaenodontidae by Van Valen (1967) following the work of Szalay (1967).

Genus *HYAENODON* Laizer & Parieu, 1838

Diagnosis. Dental formula $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{2}{3}$; M^2 with shallow groove on completely connate paracone and metacone; molars without protocone; metastyle strongly elongated, especially on M^2. Main carnassial pair M_3^2, with M_2^1 as accessory carnassials. M_3 without talonid, M_{1+2} with or without vestigial talonid (Savage, 1965).

Type species. *Hyaenodon leptorhynchus* Laizer & Parieu, 1838. Middle Oligocene (Chattian); France.

Remarks. Distinguished from other genera as follows: in *Pterodon*, M^3 is present and a small protocone and large parastyle occur on M^1 and M^2. In *Apterodon*, a protocone is present on M^1 and M^2, and M_1 possesses a prominent three-cusped talonid. M^3 is present in *Metapterodon* and M^1 and M^2 possess a strong protocone. *Leakitherium* has a strong protocone on P^4–M^2.

A complete list of species attributed to *Hyaenodon* has been given by Savage (1965). Some 36 species have been described: 9 are from North America, 3 from Asia, 20 from Europe and 4 from Africa, the latter being grouped by Savage as a distinct subgenus. Specific distinctions are based considerably on size differences. Numerous structural features have also been utilized (listed in Savage, 1965), but have nearly all proved highly variable. Many of the early European types are lost and the existing figures and descriptions are frequently quite inadequate. Of the described species, many are undoubted synonyms; several true genera probably are involved. In the absence of a greatly needed thorough revision of the genus, some attempt is made below to clarify the systematics of the Headon Beds specimens.

Hyaenodon c.f. ***minor*** Gervais, 1848–52

(Pl. 5)

1926 *Hyaenodon aimi* Cooper: 370, fig. B.

DIAGNOSIS. M_3 with talonid trace usually present but variably developed. M_1–M_2 usually with distinct cuspule at base of antero-internal paraconid face. P_1 with a single root.

HOLOTYPE. Right mandibular ramus with P_2–M_3 and alveoli of the canine and P_1. Molars badly worn. Late Eocene (Early Ludian); France. Described and figured, Gervais, 1848–52 : 129; pl. 25, fig. 9. Specimen not located.

MATERIAL. All specimens from Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff, except where stated otherwise.

B.M. 29752. Complete mandible attached at symphysis. With right canine, P_2–M_3, broken root of P_1 and alveolus of I_3; and left P_2–M_3, broken root of canine and alveolus of P_1. Teeth very badly worn—often to root level. The posterior region of both rami is complete. Labelled in British Museum (N.H.) as '*Hyaenodon hantonensis*'. Listed by Lydekker, 1884 : 444, 1885a : 25.

S.M. C31347 a-c, d, k. Probably all from same individual. Fine greenish-white sand matrix. Teeth well worn.

a. Right mandibular ramus with canine, P_4–M_3, and alveoli of P_1–P_3. M_1 is badly damaged. Posterior region preserved. Figured, Cooper, 1926 : 372, fig. A.

b. Left mandibular ramus with canine, P_2, P_4–M_3. P_3 represented by broken roots.

c. Fragment of right maxilla with P^4, damaged fragment of M^1, alveoli of P^3 and M^2. Anterior part of the zygomatic arch preserved.

d. Fragment of left maxilla with P^4–M^2 and roots of P^3.

k. Isolated left upper canine. Tip damaged.

S.M. C31344. Fragment of left mandibular ramus with P_4–M_2. Moderately worn.

B.M. 29814. Left M_3. Badly worn. Listed by Lydekker, 1885a : 26. (erroneously as right M_3).

S.M. C31346. Left P_3. Moderately worn.

S.M. C30775. Fragment of left maxilla with I^3, P^3–P^4, alveoli of the canine, M^1–M^2 and roots of P^1 and P^2. Teeth damaged. Internal surface embedded in fine greenish sand matrix.

B.M. M25073. Fragment of left maxilla with P^1–P^3, posterior alveoli of P^4 and part of the canine alveolus.

B.M. M25074. Fragment of right mandibular ramus with P_3–M_3. Moderately worn.

B.M. M13075. Fragmentary right and left mandibular rami, not attached at symphysis. Same individual. Adhering matrix of shelly orange sand. Holotype of '*Hyaenodon aimi*'. Described and figured Cooper, 1926 : 370, fig. B.

Right ramus with I_3 and the canine, P_2–M_3 and alveoli of I_2 and P_1. Tip of canine missing.

Left ramus with the canine, P_2–M_3 and alveolus of P_1. Tip of canine missing.

B.M. M25075. Fragment of left maxilla with P^2–M^2. Unworn. Upper Headon Beds (Lignite Bed), Headon Hill.

Description. The mandible is moderately elongated. The posterior mental foramen lies under the posterior root of P_3, the anterior mental foramen at a higher level, under the root of P_1. The symphysial surface is inclined at 45° to the tooth row and ends posteriorly under P_3. The posterior mandibular region is well preserved in B.M. 29752. The prominent transversely elongated condyle, situated below the level of the tooth row, is separated from a small narrow angular process by a strong notch. The angular projects downwards just below the level of the anterior mandibular margin. The coronoid is moderately well-developed with a slightly notched posterior margin. The mandibular foramen is sited markedly posteriorly, just below condyle level. The coronoid and condyloid crests are prominent.

I_2 is represented in the holotype of '*Hyaenodon aimi*' (B.M. M13075) by a small alveolus. I_3 is a small semiprocumbent tooth immediately external to the I_2 alveolus and pressed up close against the canine. I_1 may have been present but no evidence remains. Cooper (1926 : 371) stated that the incisors were not preserved.

The lower canine is large and sharp with an ovoid section. In the right ramus of S.M. C31347, this tooth is probably somewhat displaced from its alveolus. P_1 is represented by the alveolus; this single-rooted tooth was slightly separated from the canine. In S.M. C31347b, the left ramus anomalously lacks a P_1 alveolus and there is a larger gap between P_2 and the canine. Contrary to the statement by Cooper (1926 : 371, footnote) P_1 was originally present in the right ramus of B.M. 29752, as a root-filled alveolus is visible. P_2 is double-rooted, posteriorly-directed and immediately posterior to P_1; it bears a large central cusp which is postero-externally crested. There is usually a continuous internal and postero-internal cingulum, but in B.M. M13075, it is small and antero-internal in position. P_3 is similar to P_2 except that the tooth is longer antero-posteriorly and has a small posterior longitudinally crested cusp; there is no distinct posterior cingulum in B.M. M13075. P_4 is similar to P_3 but larger transversely and strongly inclined posteriorly. The cingulum is usually prominent antero-internally and postero-internally, although indistinct in B.M. M13075. Where the anterior crest of the main cusp merges with the antero-internal cingulum there is an irregular cuspule (S.M. C31347 and B.M. M25074) or a distinct cusp (S.M. C31344, B.M. M13075 and B.M. 29752).

M_1 is very small. The protoconid is slightly larger than the paraconid when unworn; these crestiform cusps are separated by a cleft. A small low talonid bears an elongated cusp. The antero-internal paraconid face (S.M. C31344) bears a small projecting cuspule which is closely pressed against the postero-internal margin of P_4; this cuspule is indistinct in B.M. M13075. On the antero-external paraconid face there is a vertical buttress pressed up against the postero-external margin of P_4. The cingulum is vestigial. In B.M. 29752, only worn rounded stumps of this tooth remain.

M_2 is similar to M_1 but of larger size. The crested paraconid and protoconid, well separated by a cleft, form good shearing facets. The antero-internal cuspule and antero-external buttress are usually well developed; the cuspule is higher than in M_1 and is not in contact with the adjacent anterior tooth. The cuspule is indistinct in B.M. M13075. The posterior talonid cusp is prominent. In B.M. 25074, this tooth is structurally similar but very small, being about the same length as M_1.

M_3 is markedly elongated in length; the crested paraconid is separated from the larger protoconid by a deep cleft; these cusps together form an effective slightly oblique shearing blade. Postero-internally, there is a small talonid rudiment in B.M. M13075 and S.M. C31347 (more strongly developed in B.M. 29752). Antero-externally, a buttress is developed as in the other molars. A trace of the antero-internal cuspule situated high on the antero-internal paraconid face is present in the least worn specimens.

Anterior to the orbits, the maxillaries have a great height, as is seen in S.M. C30775. The infra-orbital foramen is narrow and slit-like, opening above P^3 (B.M. M25073 and S.M. C30775). S.M. C31347c and d indicate a fairly narrow palatal region.

I^3 is a very small pointed tooth, slightly separated from the canine alveolus (S.M. C30775). The upper canine (S.M. C31347k, S.M. C30775 and B.M. M25073) is a large curved tooth with an ovoid section and a long vertically-striated root. P^1 (B.M. M25073) is double-rooted, elongated antero-posteriorly and situated immediately posterior to the canine; the tooth has a main cusp over the anterior root, and a strong continuous internal cingulum. P^2 is larger than P^1, but otherwise similar; it is separated from P^1 by a gap.

P^3 is separated from P^2 by a gap. This tooth is slightly larger than P^2 (B.M. M25073) and has two roots. The main cusp is crested antero-internally and posteriorly. There is a distinct crested posterior cusp, separated from the main cusp by a cleft, and a prominent internal cingulum.

P^4 (S.M. C31347c and d, and S.M. C30775) has three roots and lies immediately posterior to P^3. There is a strong protocone lobe but no distinct cusp; the transverse width is greater than the antero-posterior length. The large main cusp is separated from a small though distinct posterior cusp by a cleft; there is a small anterior cusp (more developed in B.M. M13075 and S.M. C30775 than in S.M. C31347c and d).

M^1 is much smaller than P^4 and situated immediately posterior to it; the tooth is triangular-shaped, the antero-posterior length being about the same as the transverse width. The crested anterior cusp (fused metacone and paracone) and a crested metastyle form an effective shearing blade; the cusps are separated internally by a small cleft and externally by a shallow valley. There is a small indistinct parastyle in S.M. C31347d; this is better developed in B.M. M13075.

M^2 is very similar structurally but much larger and more trenchant. The crested metastyle is tapered and elongated posteriorly; with the crested metacone/paracone, this forms internally an elongated almost vertical shear plane.

REMARKS. With the exception of B.M. M13075, most of the material listed above, for many years has been referred to the Late Eocene species, *Hyaenodon minor*. The length of the tooth row and the single-rooted P_1 appear to exclude reference to any of the other European species of Late Eocene age (listed in Savage, 1965 : 280); with the present chaotic state in the systematics of the genus, comparison of the Headon specimens with *Hyaenodon minor* seems the most reasonable course.

Cooper (1926) described a new species, *Hyaenodon aimi*, based on a well-preserved mandible from the Lower Headon Beds of Hordle Cliff. In the present work, the holotype (and only specimen) of '*Hyaenodon aimi*' is not considered specifically distinct from the other Headon Beds material. The length of the lower tooth row in the holotype of '*Hyaenodon aimi*' and in the specimens of *Hyaenodon* c.f. *minor* is almost identical (see table of measurements); dimensions of individual teeth in the two species overlap considerably. The only difference in dentition worthy of mention is the presence of a distinct cuspule antero-internal to the paraconid on M_1 and M_2 in *Hyaenodon* c.f. *minor;* this cuspule is indistinct in the holotype of '*Hyaenodon aimi*', but its presence or absence is unlikely to be of any significance.

Cooper (1926) noted the closely similar length of the lower tooth row in '*Hyaenodon aimi*' and the other Headon Beds specimens, but cited as differences the smaller more slender mandible, the closed tooth row and the curved lower margin of the mandible in '*Hyaenodon aimi.*' In particular, Cooper emphasised the differences in mandible depth below M_3 and considered the possibility of this variation being caused by differences in the sex of individuals; he concluded, by comparison with living carnivores, that the discrepancy in dimensions was too great to be accounted for in this way.

It is highly probable that these differences in mandible shape and size are due to variations in individual age. The holotype of '*Hyaenodon aimi*' is of a young individual with only a slightly worn dentition. Nearly all of the remaining Headon Beds specimens of lower dentitions exhibit greater degrees of wear, indicating more mature individuals; in these animals, increasing age has been accompanied by many changes such as a deepening of the mandible, flattening of the lower margin of the mandible and spacing of the premolars.

B.M. M25074 is rather smaller than most specimens, with a curiously small M_2. The specimen may be specifically distinct, but as little is known about intraspecific size variation in Hyaenodon species, it is best grouped at present with the other material. In general aspect, the teeth in B.M. M13075 and B.M. M25075 are slightly more slender and delicate; these specimens may represent females of the species.

TABLE 17

Measurements (in mm) of *Hyaenodon* c.f. *minor*

	P_2		P_3		P_4		M_1		M_2		M_3		P_3–M_3
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. 29814	—	—	—	—	—	—	—	—	—	—	16·1	7·0	—
B.M. 29752	9·4	4·6	12·2	5·0	—	—	—	—	(10·4)	4·8	(14·1)	—	55·5
B.M. 29752	9·4	4·7	12·3	5·1	12·4	6·4	—	—	(11·4)	—	(14·8)	(6·2)	55·5
S.M. C31347a	—	—	—	—	12·2	6·3	(7·9)	—	10·4	5·0	15·0	6·6	—
S.M. C31347b	9·6	4·7	—	—	12·8	6·1	7·6	4·2	10·5	4·8	14·5	6·3	(57·0)
S.M. C31344	—	—	—	—	12·2	6·1	7·6	4·0	10·0	5·2	—	—	—
S.M. C31346	—	—	11·3	5·0	—	—	—	—	—	—	—	—	—
B.M. M25074	—	—	9·7	5·2	11·2	5·4	7·2	4·1	7·3	4·8	11·9	5·7	45·5
B.M. M13075	9·5	5·9	10·9	5·5	11·4	6·2	8·2	5·0	11·3	6·2	14·8	7·0	56·0
B.M. M13075	10·0	5·6	11·2	5·4	11·6	5·9	8·4	4·7	11·6	5·8	14·6	6·8	56·0

	P^2		P^3		P^4		M^1		M^2		P^4–M^2
	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p
B.M. M25073	7·6	3·6	11·0	5·2	12·4	6·3	—	—	—	—	—
S.M. C31347c	—	—	—	—	—	—	11·3	10·7	—	—	—
S.M. C31347d	—	—	—	—	11·0	10·2	9·8	7·3	(14·0)	9·3	(32·5)
S.M. C30775	—	—	—	—	(12·8)	6·9	10·5	(9·7)	—	—	—
B.M. M25075	11·6	7·1	14·7	8·3	13·2	11·6	10·7	7·9	17·4	10·6	41·5

Order CARNIVORA

Family **MIACIDAE** Cope, 1880

DIAGNOSIS. P^4, M_1 carnassials as in modern carnivores. Post-carnassial teeth more or less tubercular. Metacone smaller than protocone (Matthew, 1909).

REMARKS. The family is recorded from the Middle Palaeocene-Late Eocene of North America; Late Eocene of Europe and Late Eocene–?Early Oligocene of Asia. The group has been traditionally divided into two subfamilies (Simpson, 1945 and Piveteau, 1961): Viverravinae Matthew, 1909 and Miacinae Trouessert, 1885.

Subfamily **VIVERRAVINAE** Matthew, 1909

DIAGNOSIS. Molars $\frac{2}{2}$. Antero-external cusp of P^4 and posterior accessory cusp of P_4 prominent. Elongated oval outline of M^2. M^3_3 absent. Skull much elongated. (Partly from Matthew, 1909).

REMARKS. Distinguished from the other subfamily as follows: in the Miacinae the skull is short or moderately elongated; molars $\frac{3}{3}$ and the antero-external cusp of P^4 and the posterior accessory cusp of P_4 rudimentary or absent.

The Viverravinae contains five genera:

Didymictis Cope, 1875. Middle Palaeocene-Early Eocene; North America.
Ictidopappus Simpson, 1935. Early-Middle Palaeocene; North America.
Protictis Matthew, 1937. (incl. *Simpsonictis* MacIntyre, 1962.). Middle (and Late?) Palaeocene; North America.
Viverravus Marsh, 1872. Early-Middle Eocene; North America. ?Early Oligocene; Asia.
Quercygale Kretzoi, 1945. Late Eocene; Europe.

In 1962, MacIntyre described a new genus *Simpsonictis*. More recently, MacIntyre (1965 : 3544) has separated *Protictis* Matthew, 1937, from *Didymictis* as a distinct genus: *Protictis* was considered to include *Simpsonictis* MacIntyre, 1962.

Genus ***QUERCYGALE*** Kretzoi, 1945

1965 *Humbertia* Beaumont: 142.

DIAGNOSIS. Viverravinae of medium to large size. P^4 with or without parastyle, deuterocone strong and projected. M^1 with strong parastyle, paracone robust and flattened externally, metacone smaller and more conical, no true metaconule but a paraconule present. Protocone near the anterior border bearing two crests. No hypocone. M^2 much smaller than M^1 and very elongated transversely. Lower premolars have a posterior cuspule low and trenchant. M_1 high with a metaconid higher than the paraconid. Talonid short with hypoconid trenchant and dominant. M_2 small with trigonid complete and talonid reduced and trenchant. Symphysis high and short, coronoid process more or less reduced (modified from Beaumont, 1965).

TYPE SPECIES. *Quercygale angustidens* (Filhol, 1872). ?Early Ludian (Quercy Phosphorites); France.

REMARKS. Teilhard de Chardin (1914–15) first recognised the viverravine affinities of *Viverra angustidens* Filhol, placing it in the American genus *Viverravus*. This European material was separated by Kretzoi (1945) as a new genus *Quercygale*. Beaumont (1965) placed '*Viverravus*' *angustidens* into a new genus *Humbertia* and described a new species *Humbertia helvetica* (Rütimeyer, 1862). *Humbertia* Beaumont, 1965, is synonymous with *Quercygale* Kretzoi, 1945 (Beaumont, 1966 : 282).

Quercygale differs from the other genera as follows: in *Viverravus*, the M_2 trigonid is high and the talonid is long with a distinct hypoconulid; M^1 has a hypocone (usually), a paraconule is absent and the P^4 parastyle is invariably present. *Ictidopappus* has upper teeth with a pronounced transverse elongation; the talonid of P_4 is short with a very small cusp and the lower molar talonids are basined. In *Protictis*, the M_1 and M_2 trigonid is higher and the talonid is larger and wider transversely; P_3 and P_4 have a well separated anterior cusp. As observed by Beaumont (1965), *Quercygale* appears closest to *Didymictis* but in this latter genus, the M_1 and M_2 talonid is basined and the P_4 parastyle is invariably present. Beaumont (1965) observed that apart from the absence of M_3, *Quercygale* is very similar to *Tapocyon* Stock, 1934, a miacine from the American Late Eocene. Van Valen (1967) has considered that this presence or absence of M_3 is inadequate for generic distinction, and that *Quercygale* is best considered as a subgenus of *Tapocyon*. Following this, Van Valen has concluded (1967 : 255) that . . . 'the Miacinae can no longer be unambiguously distinguished from the Viverravinae on the basis of the presence of three molars rather than two'.

Three species are recognised here:

Q. angustidens (Filhol, 1872), pl. 17, figs 33–35. Late Eocene (Bartonian-Early Ludian); France.

Q. helvetica (Rütimeyer, 1862), p. 86, pl. 5, fig. 86. Middle Eocene (Lutetian); Switzerland.

Q. hastingsiae (Davies, 1884), p. 433, pl. 15, figs 1-4. Late Eocene (Early Ludian); Britain.

Beaumont (1966) noted that *Miacis*? *macintyri* Van Valen, 1965, from the Lutetian of Germany, is very similar to *Quercygale helvetica*. Reference of *Miacis*? *macintyri* to *Quercygale* was supported by Van Valen (1967). The species is not well known (based on an isolated P^4 and M^1) and may well be synonymous with *Quercygale helvetica*.

Depéret (1917) described a new species *Procynodictis euzetensis* (later in the same work described as *Viverravus euzetensis*) from the Early Ludian of France. This species was considered by Gauthier & Favre (1948) to fall within the range of variation of '*Viverravus angustidens*'. This latter view was followed by Beaumont (1965 : 143) who recorded *Procynodictis euzetensis* as a synonym of *Humbertia angustidens*. Although the holotype of *Procynodictis euzetensis* has not been examined and Depéret's illustrations (1917, text fig. 2; pl. 24, figs 3–6) make precise comparison difficult, *Procynodictis euzetensis* is synonymised with *Humbertia angustidens* in the present work, on the authority of Gauthier & Favre, and Beaumont.

Quercygale hastingsiae (Davies, 1884)

(Pl. 6)

1884 *Viverra hastingsiae* Davies: 433, pl. 15, figs. 1–4.
1885 *Viverra hastingsiae* Davies; Lydekker: 100, figs 11–12.
1915 *Viverravus angustidens* (Filhol); Teilhard de Chardin (partim): 117.
1917 *Viverravus hastingsiae* (Davies); Depéret: 248.
1965 *Humbertia angustidens* (Filhol); Beaumont (partim): 143.

DIAGNOSIS. About the same size as *Q. angustidens*. M_1 trigonid somewhat wider and larger than talonid, with fairly blunt anterior apex; talonid larger than that of *Q. angustidens* with squared outline. Outline of upper teeth rounded; internal lobe of P^3 large; posterior margin of M^1 with strong embayment.

HOLOTYPE. B.M. 30203. Skull and mandible in occlusion. Badly crushed and damaged. The outline of the skull is preserved in fine greenish sand matrix, but only the lower part is distinct and relatively undamaged. The right and left halves of the skull have been displaced by crushing along the palatal sutures; the occluded mandibular rami are also similarly displaced relative to each other. To facilitate examination, the posterior part of the right ramus has been removed (in the past) from its original occluded position. The removed right ramus shows P_3–M_2, the exposed right maxilla and premaxilla, I–C–M^2. The upper and lower teeth anterior to P^3_3 are damaged, displaced and partly obscured by matrix. Described and figured, Davies, 1884 : 433, pl. 15, figs 1–4. Lydekker, 1885a : 100, figs 11–12. From Lower Headon Beds (Mammal/Crocodile Bed), Hordle Cliff. The only known specimen from the Headon Beds.

DESCRIPTION. P_3 is rectangular in outline and elongated antero-posteriorly, with a slight anterior narrowing. The anterior margin is squared, the posterior margin more rounded. There is a large crested central cusp and a prominent talonid which bears a small cusp. A slight postero-external and antero-internal cingulum is present. P_4 is generally similar to P_3 but much larger, and the anterior narrowing is more prominent. The talonid bears an antero-posteriorly aligned crestiform cusp and is basined internally.

The largest tooth is M_1; this has a stout bulbous trigonid which is much wider and longer than the talonid. The protoconid, the largest cusp, is opposite the metaconid; both cusps are anteriorly and transversely crested. The paraconid, the smallest trigonid cusp, is crestiform with its internal edge strongly internal in position. There is a short but wide antero-external cingulum. The small talonid is structurally similar to P_4; the internal region is slightly basined and there is an antero-posteriorly aligned crestiform cusp. M_2 is very short antero-posteriorly. The trigonid is almost as wide transversely as the talonid of M_1, with very low cusps; the protoconid is largest and slightly anterior to the metaconid. A low curved crest running from the internal paraconid to the protoconid, forms the squared anterior tooth margin. The antero-external part of this crest is badly worn; it may represent the site of a small cusp. The talonid, small and narrowing posteriorly, is well worn and shows no evidence of any cusps.

The upper teeth anterior to and including P^2 have been much displaced from their original positions. One upper incisor is preserved; it is small and simple. The upper canine is large and curved with a strong root. P^1 is embedded in matrix; it is smaller than the incisor with a single central cusp. The anterior region of P^2 is missing. The tooth has a central major cusp but is larger and more elongated antero-posteriorly than P^1. P^3 is strongly elongated antero-posteriorly and very much larger than P^2. The tooth narrows anteriorly and is dominated by a large central crested cusp. Posteriorly there is a low rounded separated cusp and a postero-external shelf-like cingulum. P^4 is triangular-shaped in outline and much larger than P^3. The tooth is dominated by a large central crested paracone; antero-externally this falls as a crest towards a low rounded parastyle. There is a low rounded protocone which is larger than the parastyle. The anterior margin between parastyle and protocone is strongly embayed. The crestiform metacone is separated from the paracone by a deep cleft which continues externally as a narrow valley; these cusps together form a sharp oblique postero-internal shearing edge. There is a small distinct antero-external cingulum and a faint postero-external cingulum.

M^1 is the same width transversely as P^4. The metacone is directly posterior to the larger paracone; a posterior metacone crest curves antero-externally along the external tooth margin to the parastyle. The crested protocone is crescentic in shape, an anterior crest running antero-externally towards the paracone; a low paraconule is developed on this crest just antero-internal to the paracone. The parastylar area extends externally as a wing which is separated from the postero-external area by a small embayment. The parastyle is crestiform; it is joined to an external paracone crest. There is a distinct internal and antero-internal cingulum.

M^2 is much smaller than M^1 and a little smaller than P^3. The ovoid tooth lies obliquely in the tooth row. The antero-external margin is in contact with M^1 just posterior to the M^1 metacone. The crown of the tooth is badly damaged and no details can be discerned.

REMARKS. Teilhard de Chardin (1915 : 117, footnote 1) considered that '*Viverravus*' *hastingsiae* was synonymous with '*Viverravus*' *angustidens*. Depéret (1917 : 248) recorded several differences, on the basis of which he believed the two species to be distinct. Gauthier & Favre (1948 : 116) emphasised the larger M_1 talonid of '*Viverravus*' *hastingsiae* but were uncertain whether this merited specific separation. More recently Beaumont (1965 : 143) on the evidence of the more elongated M_1 talonid, considered '*Humbertia*' *hastingsiae* as a distinct subspecies of '*Humbertia*' *angustidens*. Depéret's view is followed here. In addition to the considerably more elongated talonid of M_1, the P^3 of *Quercygale hastingsiae* (from comparison with illustrations of *Q. angustidens*) has a smaller internal heel as Depéret observed. Although this single specimen from the Headon Beds may be aberrant, it seems reasonable at present to regard it as specifically distinct.

TABLE 18

Measurements (in mm) of *Quercygale hastingsiae*

	P_3		P_4		M_1		M_2	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30203	7·0	2·8	9·1	3·7	9·7	6·2	5·1	3·6
	P^3		P^4		M^1		M^2	
	a-p	trs	a-p	trs	a-p	trs	a-p	trs
B.M. 30203	7·8	—	11·3	—	6·7	—	—	—

IV. CORRELATION AND AGE OF THE HEADON BEDS

Although there is general agreement concerning the broad correlation of Upper Eocene and Lower Oligocene deposits in Europe, no unanimity has been reached yet regarding the detailed correlation of marine and non-marine sediments in the different depositional basins. One particular problem is the exact siting of the Eocene/Oligocene boundary. The situation is hindered by a confused stage and substage terminology, which despite many recent attempts at clarification by authors, has still to be resolved.

It is not intended here to present a critical review of this problem, detailed aspects of which have been considered recently by Rey (1964), Krutzsch & Lotsch (1964), Blondeau, Cavelier, Feugueur & Pomerol (1965), Thaler (1966), Denizot (1968), Cavelier (1968), Curry, Gulinck & Pomerol (1969) and others. The complete mammalian fauna of the Headon Beds has not yet been studied in detail, and authoritative use of the mammals in correlation and dating is clearly premature. Nevertheless, in view of the importance of the Headon Beds in current stratigraphical research, some interim conclusions are presented here.

The exact age of the Headon Beds and indeed of most of Forbes' 'Fluvio-marine series' has long been controversial. The uppermost beds of the British succession, the Hamstead Beds, are generally accepted to be Oligocene in age. No unanimity has been reached regarding the age of the underlying Bembridge, Osborne and Headon Beds. Three schemes have been proposed in the past for the age of the Headon Beds; two schemes are supported currently by European stratigraphers and palaeontologists, but the third, that proposed by Reid & Strahan (1889) is now obsolete.

Reid & Strahan (1889) and Arkell (1947) considered that the Lower, Middle and Upper Headon Beds were Oligocene (Lattorfian of Arkell) and the underlying Barton Beds were uppermost Eocene. The Eocene/Oligocene boundary lay at the base of the Lower Headon Beds. This view, in which is emphasised the general change from marine to brackish and freshwater conditions at the beginning of Lower Headon times, has not found further support.

In a currently held view, supported traditionally by most British workers, the Lower Headon Beds are considered as uppermost Eocene (Bartonian) and the Middle and Upper Headon Beds are Oligocene (Lattorfian, Tongrian). The Eocene/Oligocene boundary is placed, therefore, at the base of the Middle Headon Beds. This view, based on correlation by mollusca and foraminiferida of the Middle Headon Brockenhurst Bed with the type Lattorfian (Lower Oligocene) of Germany, has been adopted by Wrigley & Davies (1937), Bhatia (1955), Denizot (1957, 1968), Curry (1958a, 1966), Chandler (1961a, 1963), Rey (1964), Franzen (1968) and others.

In the second currently supported arrangement, the Lower, Middle and Upper Headon Beds are placed together with the Barton Beds in the Upper Eocene (Lower Ludian). This was adopted by Stehlin (1910) and followed more recently by Krutzsch & Lotsch (1964), Blondeau, Cavelier, Feugueur & Pomerol (1965), Thaler (1966) and Cavelier (1968). In this scheme, the Eocene/Oligocene junction is placed at some position above the Upper Headon Beds. Stehlin (1910) on the basis of what he believed to be a fundamental break in the mammal faunas ('grande coupure'), considered that the Eocene/Oligocene junction in Britain should be placed at the base of the Hamstead Beds; this has been followed more recently by Krutzsch & Lotsch (1964), Blondeau *et al* (1965) and Cavelier (1968). Thaler (1966) preferred to place the boundary at the base of the Bembridge Beds.

Stehlin (1910) compared the mammalian fauna of St.-Hippolyte-de-Caton (=Euzet-les-Bains) with the Lower Headon Beds, considering them Lower Ludian in age.

The same faunas were compared by Depéret (1917) who also assigned them a Lower Ludian age. Stehlin (1910) also compared the mammalian fauna of Montmartre with a similar fauna from the Bembridge Limestone; he considered these faunas to be Upper Ludian in age. According to Stehlin (1910) the fauna from the Bembridge Marls was similar to that from the Bembridge Limestone. He observed that the Upper Ludian (Bembridge Beds) fauna differed from that of the Lower Ludian (Lower Headon Beds) fauna by the extinction of several species and the arrival of several forms unknown in the Lower Ludian. Stehlin's correlations of the Lower Ludian faunas of Euzet-les-Bains with the Lower Headon Beds, and the Upper Ludian faunas of Montmartre with the Bembridge Limestone, have now become well established.

Recently, Thaler (1965, 1966) proposed to replace the old classification by a series of seven zones defined by theridomyids. Although some of Thaler's zones transgress the traditional stratigraphical subdivisions, the Euzet zone, Montmartre zone and Ronzon zone correspond exactly with the Lower Ludian, Upper Ludian and 'Sannoisian' respectively.

Stehlin (1910) noted that as the faunas of the beds above the Lower Headon Beds and below the Bembridge Limestone were poorly known, it was not possible in Britain to determine the precise junction of the Lower and Upper Ludian faunas. More recently, Krutzsch & Lotsch (1964) grouped the Upper Headon Beds and Osborne Beds in the Montmartre zone with the Bembridge Beds; for them, the junction of Lower and Upper Ludian faunas lay at the base of the Middle Headon Beds.

The mammalian fauna obtained recently from the Upper Headon Beds appears to be similar to that from the Lower Headon Beds and apparently distinct from the Bembridge fauna. While the sample from the Upper Headon Beds is clearly still incomplete, the Upper Headon Beds, on present evidence, should be grouped, at least provisionally with the Lower Headon Beds in the Upper Eocene (Lower Ludian). The Upper Headon fauna should be placed in the Euzet zone, rather than the Montmartre zone as suggested by Krutzsch & Lotsch (1964). It follows that, on the basis of the mammalian faunas, the traditional British practice of siting the Eocene/Oligocene boundary at the base of the Middle Headon Beds, cannot be sustained. This present view is in agreement with Martini (1970) whose study of calcareous nannoplanckton from the Brockenhurst Bed, has indicated that the Brockenhurst Bed is uppermost Eocene in age, and not equivalent to the type Lattorfian (Lower Oligocene).

The Eocene/Oligocene boundary therefore, must be situated at some position above the Upper Headon Beds. Owing to the poorly known mammalian fauna, the exact stratigraphical position of the overlying Osborne Beds is uncertain at present. However, study of this fauna, together with the fauna of the Bembridge Beds, currently in progress by Mr A. Insole at the University of Bristol, may clarify this situation.

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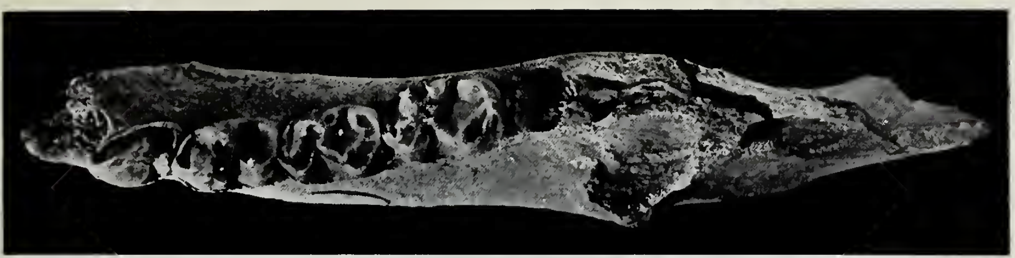
PLATE 1

×2 approx.

Adapis magnus Filhol. Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P_3–M_2. B.M. M10260. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Fragmentary left maxilla with P^2–P^3, M^1–M^3. B.M. M3572. Occlusal view.



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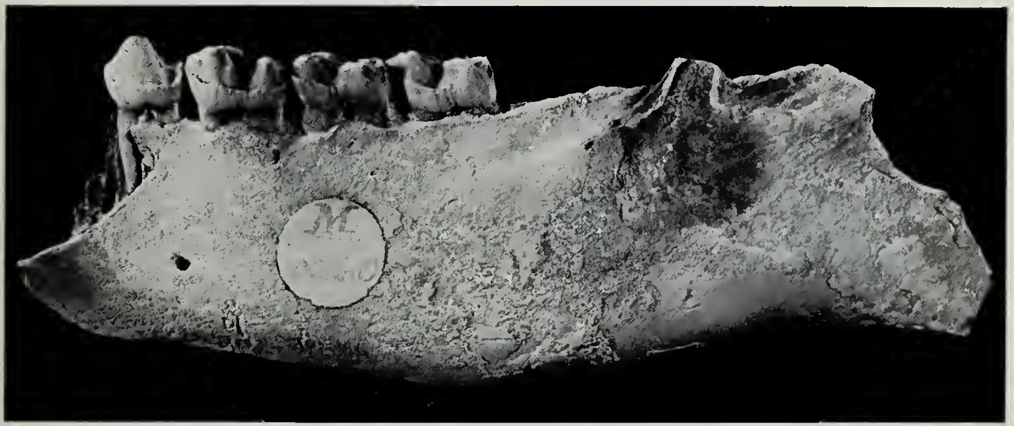

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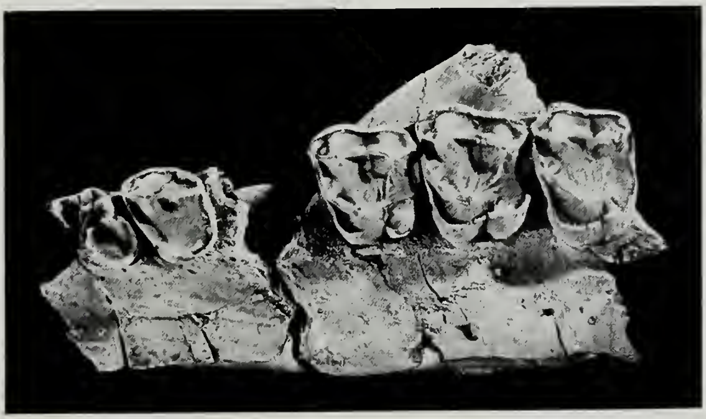

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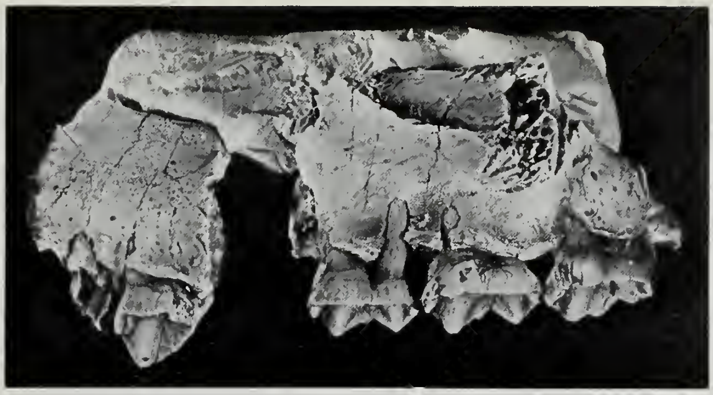
PLATE 2

× 2 approx.

Fig. 1. ***Adapis magnus*** Filhol. Fragmentary left maxilla with P^2–P^3, M^1–M^3. B.M. M3572; External view. Specimen supported in plasticine. Lower Headon Beds, Hordle Cliff.

Figs 2–3. ***Adapis parisiensis*** (Blainville). Fragmentary associated mandibular rams. Right ramus with P_2–M_1, M_3, left ramus with M_1–M_3. F.C.S. 7. Upper Headon Beds, Headoi. Hill. Fig. 2. Occlusal view of both rami. Fig. 3. External view of right mandibular ramun



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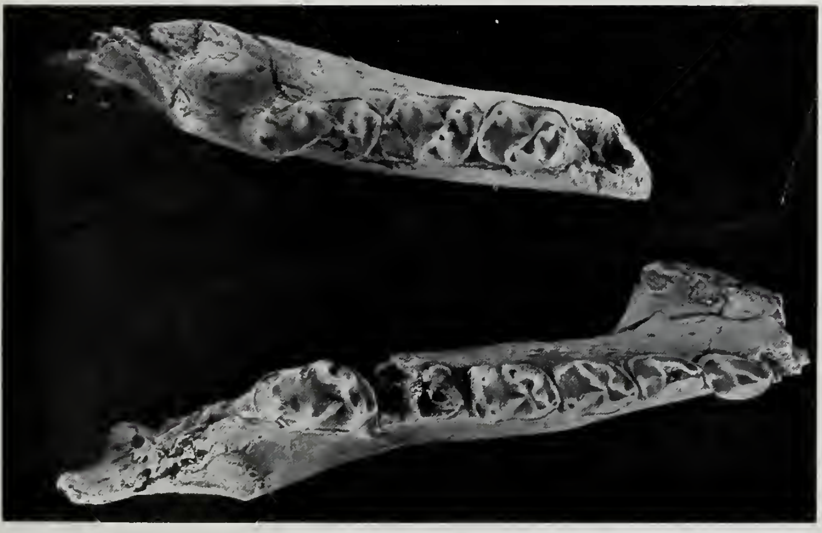

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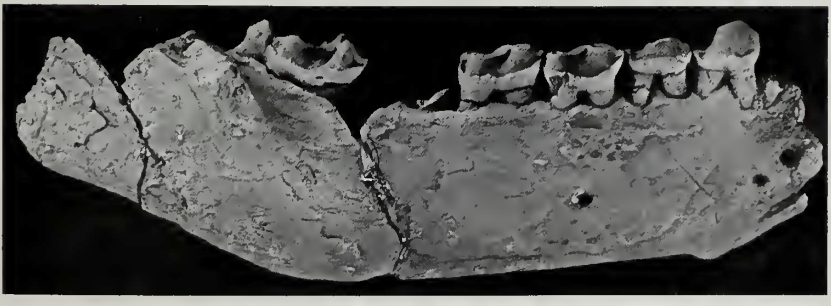

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PLATE 3

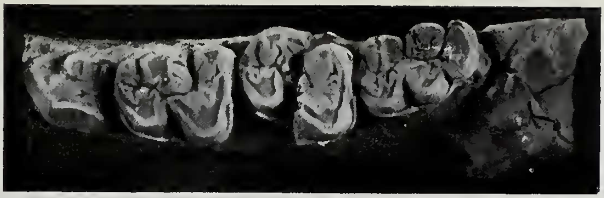
×4 approx.

Microchoerus erinaceus Wood. Holotype (B.M. 25229).

Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P_4–M_3. B.M. 25229 (1). Wax reconstruction of anterior and posterior regions not illustrated. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Palatal fragments with an almost complete upper dentition. B.M. 25229 (2). Occlusal view. Right I^2 is a plaster reconstruction.



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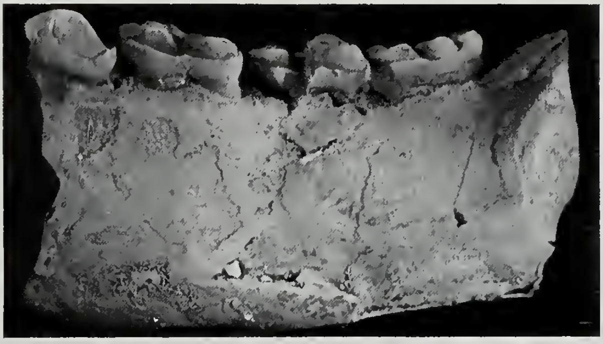

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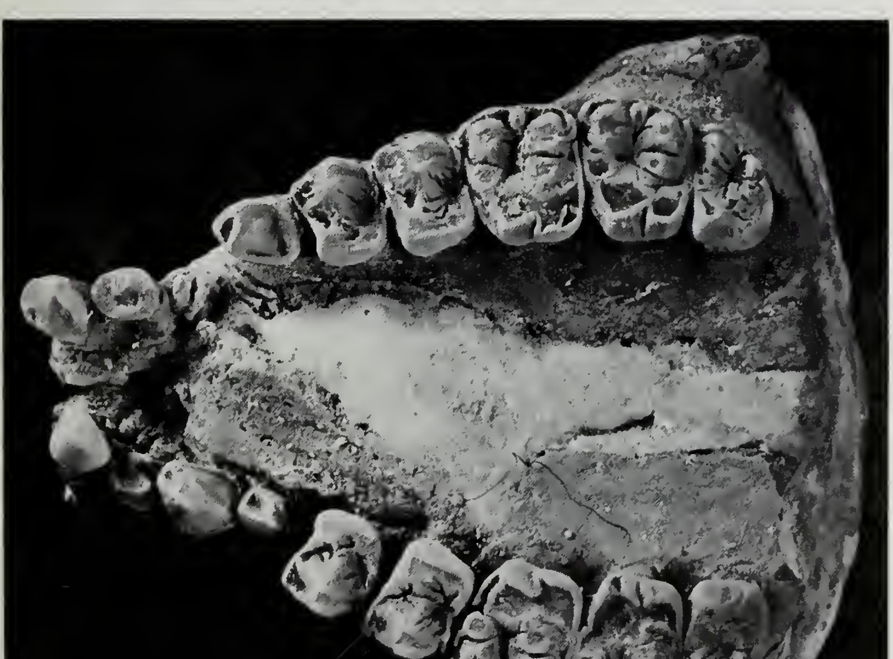

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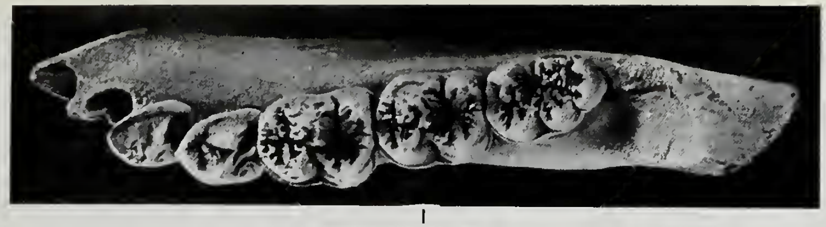
PLATE 4

× 4 approx.

Microchoerus erinaceus Wood. Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary left mandibular ramus with P3–M3. S.M. C9681. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Fragmentary left mandibular ramus with M1–M3 and complete posterior region. External view. S.M. C9672.



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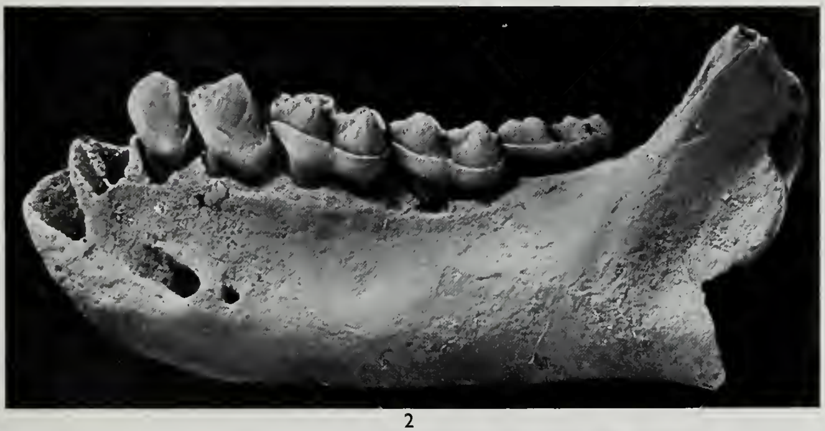

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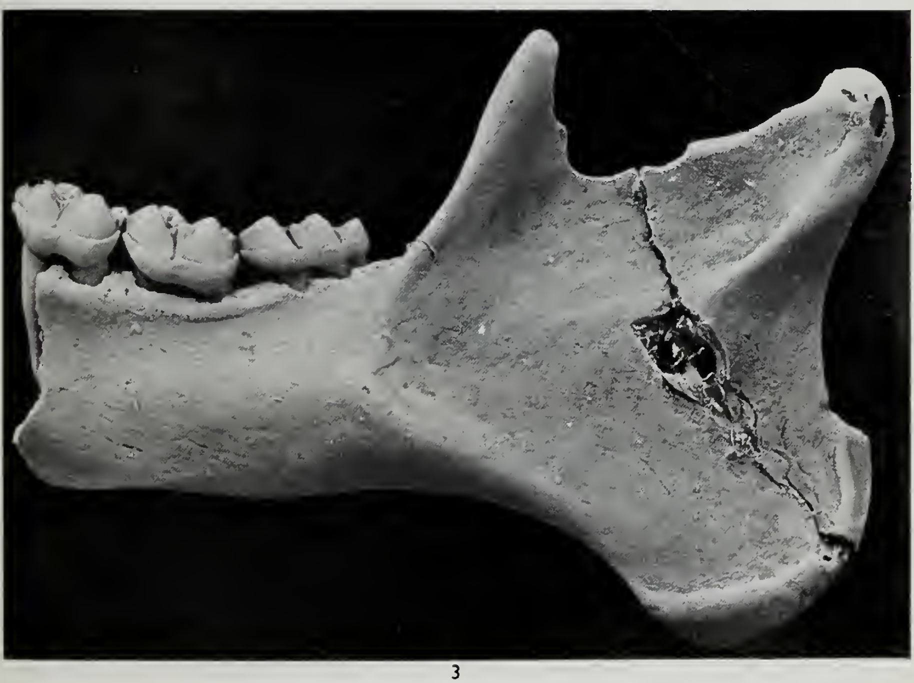

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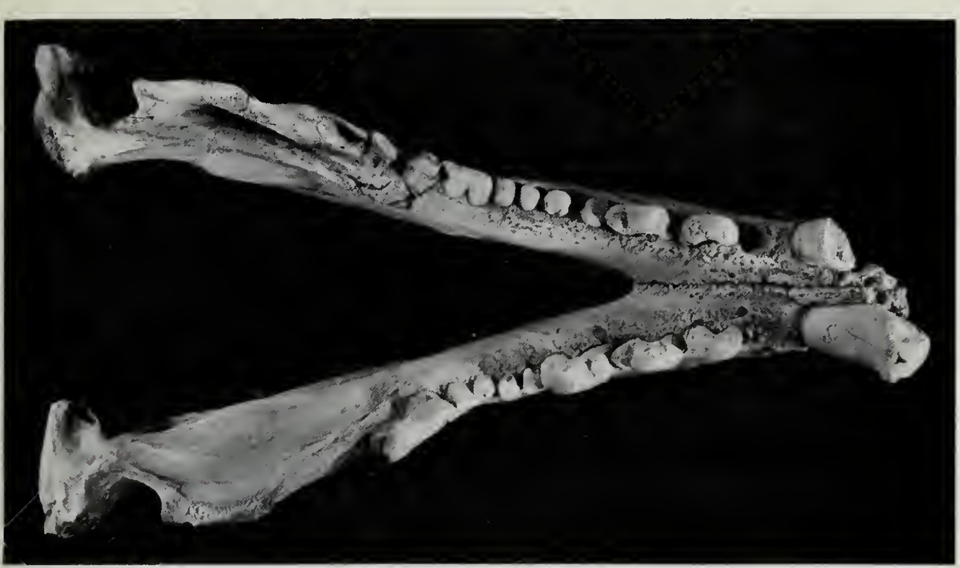
PLATE 5

Hyaenodon c.f. ***minor*** Gervais

Figs 1–2. Mandible with C, P_2–M_3 of both sides. B.M. 29752 ×0·8 approx. Lower Headon Beds, Hordle Cliff. Fig. 1. Occlusal view of both rami. Fig. 2. External view of right ramus.

Figs 3–4. Fragmentary left maxilla with P^2–M^2. B.M. M25075 ×1 approx. Upper Headon Beds, Headon Hill. Fig. 3. Occlusal view. Fig. 4. External view.



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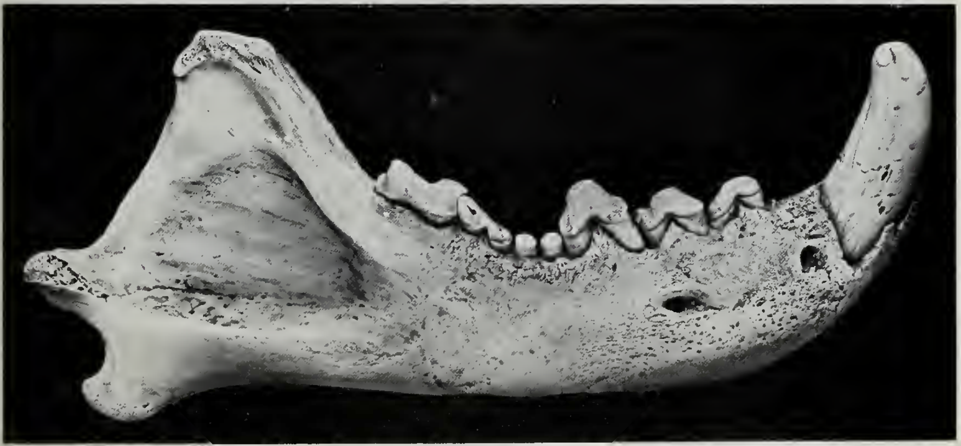

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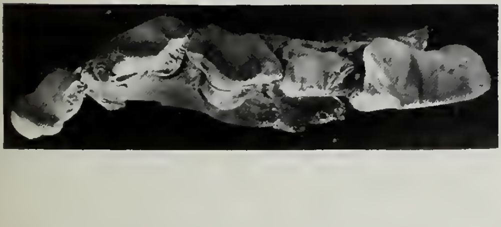


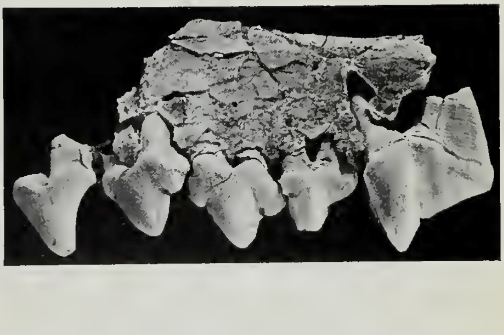


PLATE 6

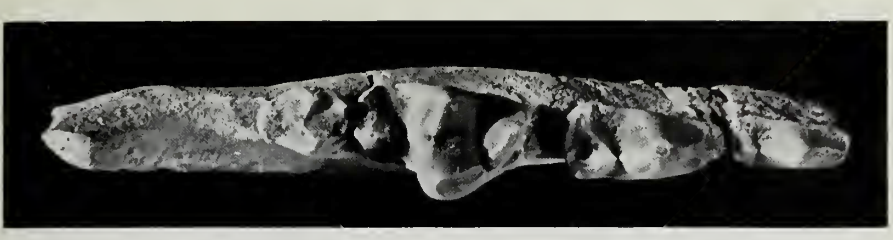
×2·5 approx.

Quercygale hastingsiae (Davies). Holotype (B.M. 30203)

Lower Headon Beds, Hordle Cliff

FIGS 1–2. Fragmentary right mandibular ramus with P_3–M_2. Fig. 1. Occlusal view. Fig. 2. External view.

FIG. 3. Right P^3–M^2; Occlusal view.



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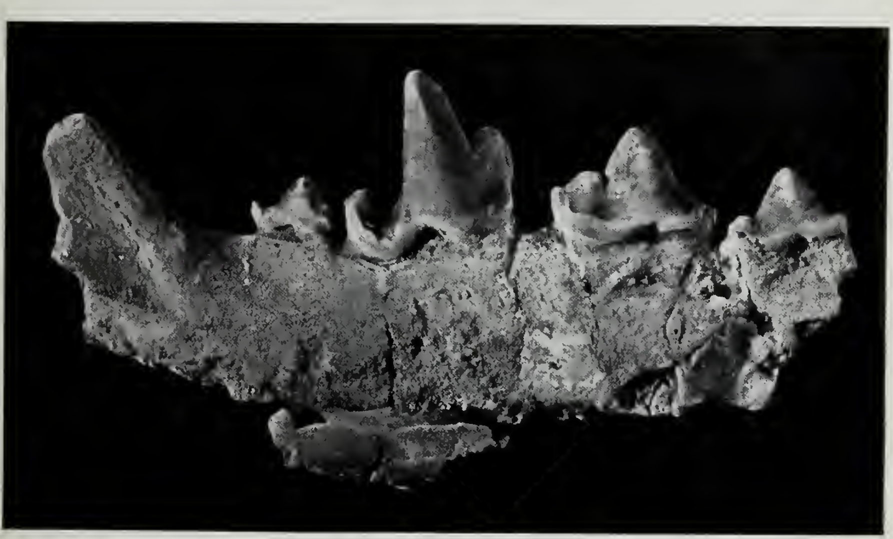

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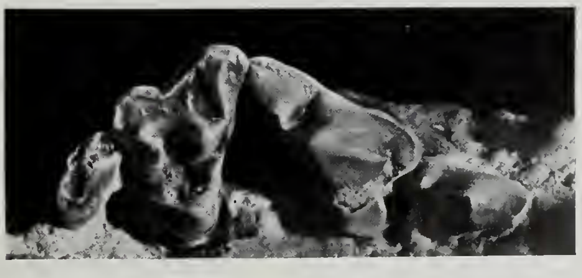

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